A TEXTBOOK OF BOTANY

REVISED

VOLUME THREE

ECOLOGY

COULTER — BARNES — COWLES

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A TEXTBOOK *of* BOTANY

FOR COLLEGES AND UNIVERSITIES

By

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VOLUME THREE. ECOLOGY

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PREFACE

THE study of plants may be approached from so many points of view that every laboratory has developed its own method of undergraduate instruction. No laboratory attempts to include all the phases of work that may be regarded as belonging to botany; and therefore each one selects the material and the point of view that seem to it to be the most appropriate for its own purpose. For many years the Hull Botanical Laboratory at the University of Chicago has been developing its undergraduate instruction in botany to meet its own needs. Freed from the necessity of laying special stress upon the economic aspects of the subject, and compelled to prepare students for investigation, it seemed clear that its selection must be the fundamental facts and principles of the science. Its endeavor has been to help the student to build up a coherent and substantial body of knowledge, and to develop an attitude of mind that will enable him to grapple with any botanical situation, whether it be teaching or investigation. It has been thought useful to present this point of view in the present volume. The material of course is common to all laboratories, but its selection, its organization, and its presentation bear the marks of individual judgment.

The three volumes of this series represent the three general divisions of the subject as organized at the Hull Botanical Laboratory. They are felt to be the fundamental divisions which should underlie the work of most subdivisions of botanical investigation. For example, a study of the very important subject of plant pathology must presuppose the fundamentals of morphology and physiology; paleobotany is, in part, the application of morphology and ecology to fossil plants; and scientific plant breeding rests upon the foundations laid by morphology, physiology, and ecology. In our selection for undergraduate instruction, therefore, we believe that there has been included the essential foundation for most of the varied work that is included to-day under botany.

We recognize that the presentation of the three subjects here included is very compact, but the book is not intended for reading and

recitation. The teacher is expected to use it for suggestive material and for its organization; the student is expected to use it in relating his observations to one another and to the general points of view that the book seeks to develop. There is a continuity of presentation in each book. Random selection of material may miss the largest meaning. For example, in the part on morphology, the thread upon which the facts are strung is the evolution of the plant kingdom, and each plant introduced has its peculiar application in illustrating some phase of this evolution. When certain unconnected groups are selected for laboratory study, therefore, the intervening text should be read.

It is important to emphasize the fact that the book has been prepared for the use of undergraduate students. It does not represent our conception of graduate work, which should include much that is omitted here. For example, the graduate student should make much larger use of original sources of information, which would involve an extensive citation of literature far beyond the needs of the undergraduate. Still less has this book been written for our professional colleagues, who will notice what they may regard as glaring omissions. Such omissions must be taken to express a deliberate judgment as to what may be omitted with the least damage to the undergraduate student. The motive is to develop certain general conceptions that are felt to be fundamental, rather than to present an encyclopedic collection of facts. This purpose has demanded occasionally also a greater apparent rigidity of form in general statements than is absolutely consistent with all the facts. In presenting the material to students who had not yet developed perspective, it was necessary to choose between a clear and important conception on the one hand, and a contradiction of large truths by isolated facts on the other, which might result in confusion. For the same reasons, the extensive terminology of the subject has been kept in the background as much as possible. Definitions usually are made an incident to the necessary introduction of terms. It is assumed that in so far as the definite application of a term may not seem clear, the student will find a compact definition in the current dictionaries.

For the benefit of the teacher and of our professional colleagues, it should be stated that much attention has been given to the avoidance of any phraseology that might involve a teleological implication. It has not been possible to avoid such phrases in all cases without introducing clumsiness of expression or breaking the continuity of

some important series of structures or events. It should be kept in mind, therefore, that all teleological implications of language that remain are disavowed.

It seems hardly necessary to say that most of the material presented in the book has been worked over by classes repeatedly. Some new matter has been developed incidentally in all the parts in connection with ordinary laboratory and field work. Especially in Volume Three have many scattered observations and some new points of view been included. There has been no intention to include any formal contribution, but merely to present in general outline some of the material worked over by undergraduates, some of the results of investigation already published in contributions from the laboratory, and some observations and conclusions that hardly seemed to justify separate publication. Provision has been made for students with more interest or more time than usual to get a somewhat larger view, by including in smaller type further details of structure, additional illustrative material, and suggestive theories.

The selection and preparation of the illustrations for these volumes were under the efficient direction of Dr. W. J. G. Land. Most of the illustrations are original, and many of them were made by Miss Anna Hamilton, an artist to whom great credit is due. Miss Anna M. Starr also contributed drawings to Volume Three. Those that have been copied or adapted are appropriately credited to the original sources.

In the preparation of this edition of Volume Three the general organization and scope of material in the original edition have been retained. On many pages no alterations have been necessary. Additions have been made where the advances of plant ecology during the past two decades have demanded them. Such changes and additions have had the approval of the original author but for any errors that have persisted in spite of all efforts to eliminate them the present author assumes full responsibility. In correcting them the authors will welcome the assistance of the wider circle of readers to whom the book now goes.

In the revision of the citations of literature particular attention has been given to contributions in the English language and to those that have summarized various phases of the subject.

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ECOLOGY

INTRODUCTION

The scope of ecology. — *Ecology* is still a very young science although it has already a great body of data and theories whose validity is well established. The systematic organization of these data is, however, very incomplete. It is not possible as yet to mark out its limits, for it overlaps to a greater or less degree every other field of biology, and of physiography and geology as well. Speaking broadly, ecology considers organisms in relation to their environment. Somewhat more precisely, ecology is that phase of biology that endeavors to explain the origin, variation, and rôle of plant or animal structures, and the origin, structure, and variation of plant and animal communities.

Plant ecology has a twofold aspect: the one considers the individual organism and its component parts as related to environment; this, since it overlaps morphology and physiology, may be called *morphological* and *physiological ecology*, or the ecology of plant structure and behavior. It has also been termed *autecology* since it is concerned with the individual organism. The other aspect considers plants *en masse* as related to soil, to climate and to one another; this, since it overlaps physiography, may be called *physiographic ecology*, or the ecology of vegetation. Since it considers plant communities, it has also been termed *plant sociology* or *synecology*. Morphological and physiological ecology consider the same materials as do morphology and physiology, but largely from a different point of view. Morphology deals with structure and physiology with behavior, whereas ecology relates both structure and behavior to external conditions, paying attention chiefly to the cause and the significance of environmental variations. Morphology and physiology are essentially laboratory sciences, while ecology is in the main a science of the field, treating organisms as they grow in nature.

Since ecology overlaps various sciences, it is less a simple science than a science complex; its adequate study presupposes a foundation in the

basic principles of physics, chemistry, morphology, and physiology, and, in the case of physiographic ecology, of taxonomy, physiography, geology, and meteorology as well. Partly because of its complexity and partly because of its imperfect organization, it is impossible to present all its materials, even in elementary fashion, within the compass of such a book as this. Consequently, it has been thought wise to center attention upon morphological and physiological ecology, since this aspect is more in harmony with the other volumes in this series and is better suited for elementary presentation to students of botany.

Terms. — While most of the terms employed are defined where first introduced or used extensively, a few are of such general employment as to justify consideration here. Since water generally is regarded as the most important factor, the commonest ecological classification of plants is into hydrophytes, mesophytes, and xerophytes. *Hydrophytes* are plants of water or of wet soil; *xerophytes* are plants of dry areas, such as deserts, dry rocks, and dry sand; and *mesophytes* are plants of soils intermediate as to moisture. The term xerophyte has caused much confusion, because many plants growing in soils of intermediate or abundant moisture have structures resembling those found in plants of dry soils and climates. The most conspicuous instances of such plants are found in alpine and arctic regions, in salt marshes, and in peat bogs, and such terms as *bog xerophytes* and *salt marsh xerophytes* are in common usage. The current theory is that deserts, rocks, and sandy areas are *physically dry*, that is, lacking in water; whereas salt marshes, peat bogs, and many alpine and arctic habitats are *physiologically dry*, that is, the water even if abundant is unavailable. In arctic and alpine regions this is because of low temperatures, and in salt marshes it is because of the high osmotic pressure of the medium, while in the case of bogs various theories have been suggested.

The term *variation* is employed in its broader sense of difference or diversity, rather than in its narrower evolutionary sense of " deviation from type." *Ecological variation*, or diversity produced through the influence of external factors, frequently is contrasted with *taxonomic variation*, where there is had in mind diversity between allied forms rather than actual modification; that is, the former is necessarily dynamic, whereas the latter may be relatively static. Frequent use is made of the term *external factors*, as opposed to *internal* or *inherent factors*. By the former are understood such factors as are outside the

plant, and by the latter, such factors within the plant as are hereditary. There is another class of factors, known as *correlative factors* or *correlations* which reside within the plant, but are external to the organ affected and are not hereditary. For example, the influence of a stem upon the development of its lateral branches is correlative; so far as the branches are concerned, this is quite as external as are such factors as light and humidity.

Scarcely second in importance to the terms used are the terms avoided. The standpoint of this book, contrary to that of many previous ecological treatises, is that of mechanical causation rather than of teleology and adaptation (see p. 465 for a discussion of ecological philosophy), hence many familiar terms are here avoided; among such are words like *adaptation*, *adjustment*,[1] *accommodation*, and *regulation*, purposive words which are here replaced by the expression *advantageous reaction*, thus recognizing that some activities are indifferent or disadvantageous. Two of the commonest and most insidious words conveying teleological implications are *to* and *for*, in such sentences as "winged seeds are a mechanism *for* dispersal" and "plants close their stomata and develop cutin *to* check transpiration." Words implying forethought, such as *reserve* and *storage*, usually are omitted, as are anthropomorphic words in general, particularly those suggestive of emotion (such as *hydrophile*, *xerophile*, *heliophobe*, *geophilous*, *entomophilous*). Less objectionable, perhaps, but rather fanciful, are words or expressions which imply that plants, like men, try to do things, as conveyed in the familiar expression, *struggle for existence*, and in such words as *success*, *failure*, or *competition*, as applied to plant behavior. Some words, in themselves unobjectionable, have been used so generally with teleological implications, that they mostly are omitted; for example, the word *function* has been employed so often in the sense of purpose that *rôle* is used wherever feasible; similarly, *reaction* usually is employed in place of *response*, though theoretically the latter word is quite as good. The attempt is made generally to use words that are equally applicable in physics and in chemistry; especially is this attempt worth while, because ecology, more than any other phase of biology, has suffered from the unrestricted use of anthropomorphic similes and teleological fantasies.

[1] Such terms as adaptation and adjustment, when used in the sense of a state, rather than in the sense of a process, are relatively unobjectionable, but in view of their large past use in the latter sense, they are liable to lead to confusion and hence are omitted in all senses.

It is realized that language lags behind ideas, that we still speak of the heart as the seat of the emotions, and of the rising and the setting of the sun, so it is likely that some teleological expressions remain. Some words of which frequent use is made, such as *advantage* or *efficient*, may to some appear teleological. Such terms, however, are employed in the sense of the perpetuity of the species. Any structure or reaction that favors the extended duration of an individual or of the race to which it belongs is regarded as advantageous, while any structure or reaction that is detrimental to such duration is regarded as disadvantageous. In this sense such a word as advantage is not teleological, for it might be thus employed with reference to many inorganic substances.

The arrangement of the material. — In the following pages the material is grouped on the basis of *structure*, the fundamental plant parts being regarded as roots, leaves, stems, and reproductive organs. The same material might be grouped under the head of *behavior*, including such topics as absorption, conduction, synthesis, transpiration, reproduction, and the like; or again, the material might be grouped under the head of *factors*, as light, heat, water, etc. The method here used, that of classification by structure, seems best suited to the present state of ecological knowledge, where structure alone is approximately sure. In many cases, organs have no known rôle, and still more frequently a given organ has two or more rôles, thus making a classification by behavior difficult and repetitious; furthermore, classification by behavior places too much emphasis upon the employment of organs and is likely to lead to teleological mysticism. The classification of ecological data by factors is fundamentally sound, but is at present practically impossible, owing to the paucity of known facts as compared with those that are unknown.

The differentiation of the plant body. — While the material here presented is classified chiefly under *roots*, *leaves*, *stems*, and *reproductive organs*, it is not assumed that there are hard and fast lines between these plant parts. The evolutionary hypothesis presupposes transitions between all organs, and there are many evidences of intergradations even between the most diverse plant parts. In the lowest plants the body is an undifferentiated *thallus*. In algae and fungi there is seen the first conspicuous differentiation, that between vegetative and reproductive organs. In the thallose liverworts the vegetative part becomes differentiated into a green food-making aerial portion and a colorless rootlike subterranean portion; in the leafy liverworts and in

mosses the aerial vegetative portion is differentiated still further into stems and leaves. Certain liverworts exhibit all gradations between thalli and leafy stems. Even in the seed plants, where differentiation into roots, stems, and leaves seems relatively fixed, there are cases where the exact nature of certain organs is subject to dispute (as in the rhizophores of *Selaginella*, the plant body of *Utricularia*, and the spines of cacti).

The chief characteristics of roots, leaves, and stems. — The root generally is a descending, irregularly branching axis, while the stem generally is an ascending, regularly branching axis, possessing *nodes* and *internodes*, and bearing leaves as lateral members and reproductive shoots as lateral or terminal members; branch shoots commonly arise in the leaf axils. Branch roots arise from within (*endogenously*), contrasting with branch shoots which arise at the exterior (*exogenously*). Young roots possess a root cap which ensheathes the growing tip, and strands of xylem and phloem alternate in the same circumference; the central region is occupied by conductive tissues, and the epidermis is ephemeral. Young stems contrast with young roots in that the xylem and phloem form continuous or interrupted cylinders about the pith, the phloem commonly being outermost; the epidermis is much less ephemeral than in roots. Stems and roots commonly are *radially symmetrical*, possessing an infinite number of vertical planes of symmetry, while leaves are *dorsiventrally symmetrical*, possessing a single plane of symmetry.

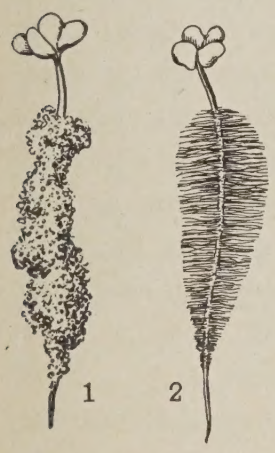
The preceding distinctions between roots, stems, and leaves are general but not universal. For example, some roots are exogenous in origin and some stems endogenous. Not all roots have root caps. Some roots bear buds which are able to develop into leafy shoots; shoots borne on roots are not necessarily subtended by leaves. Old roots and stems may be indistinguishable in structure; many stems and roots are without radial symmetry, and sometimes there is but a single plane of symmetry, as in most leaves; some leaves, however, are all but radially symmetrical (p. 143). These and similar exceptions indicate sufficiently the intergradations between these organs. Indeed, it is doubtful if a single characterization can be made that always holds; occasionally it is only by a majority test of its characters that the nature of an organ may be determined. Sometimes one or more of the plant parts may be missing, as the roots in *Salvinia*, and as both leaves and roots in *Wolffia;* many rosette plants, as the dandelion, are

practically stemless. Thus, such terms as roots, leaves, stems, and reproductive organs are convenient words rather than fundamental categories. Here, as in every branch of knowledge, all schemes of classification confessedly are artificial, and yet an orderly arrangement of material is necessary. Even where the various plant organs are well differentiated, they are not treated rigidly in the following pages, but each subtopic is considered where it seems the most appropriate; for example, food manufacture is treated under leaves, conduction and mechanical support under stems, and food accumulation under seeds, while vegetative reproduction is considered chiefly under stems.

CHAPTER I — ROOTS AND RHIZOIDS

1. SOIL ROOTS AND ROOT HAIRS

Root hairs. — *General remarks.* — Most land plants possess roots which branch freely and penetrate the soil in all directions. While the main roots of adult plants often are large and stout, the ultimate branches are slender and give rise to very delicate organs, the root hairs. The chief rôle of soil roots is in connection with absorption and anchorage. The entire root system is concerned in the latter, but the admission of water and salts is restricted practically to the very youngest portions.



FIGS. 1, 2. — Seedlings of mustard (*Brassica alba*): 1, a seedling dislodged from the soil, showing particles of earth adhering to the root hairs, the root tip being free from hairs or attached particles; 2, a seedling grown in moist air, showing a primary root with its zone of root hairs, the younger hairs toward the tip being progressively shorter; the seed-leaves (cotyledons) rise above the soil, illustrating epigaean germination (p. 452). — After SACHS.

The structure and rôle of root hairs. — Root hairs are extensions of the epidermal cells of roots (figs. 1–3, 6), most such cells possessing the capacity of developing hairs, though many are without them.[1]

The walls are thin, readily permitting the entrance of water and solutes. The outer portion of the wall is composed of pectic substances, often of calcium pectate. The inner layer of the wall is supposed to be of cellulose. Though root

[1] In various pteridophytes (as *Azolla*) and monocotyls, however, hairs arise only from special small cells rich in protoplasm.

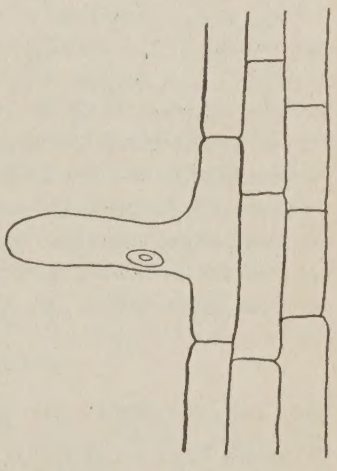
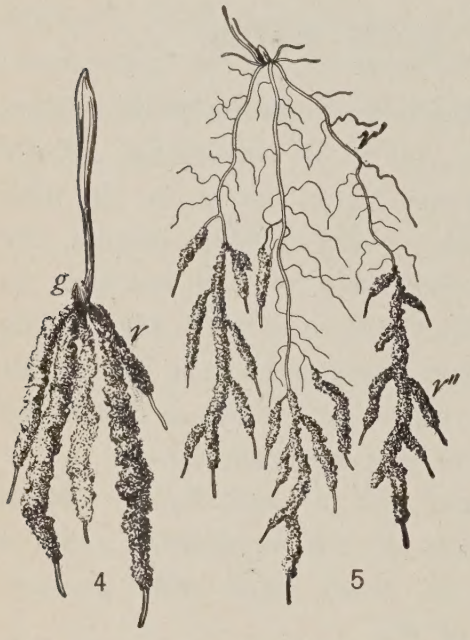


FIG. 3. — A longitudinal section through the outer portion of a root of corn (*Zea mays*), showing a root hair arising as an outgrowth of an ordinary epidermal cell; the nucleus has migrated into the root hair.

hairs vary greatly in length and abundance they usually range from one to four millimeters in length and as many as four hundred may develop within a square millimeter of root surface. While the entire root epidermis is permeable to water and solutes, the chief advantage derived from root hairs seems to be the increase of permeable surface, which sometimes is as much as five or ten times that of a hairless root of equal size. The youngest hairs emerge a short distance behind the tip; farther back they are of mature size, and still farther back they are withered and dead. Indeed, the entire epidermis is soon sloughed off, and the hypodermis (here called the *exodermis*) becomes the outer layer of the root, which through cutinization is thenceforth relatively impermeable to water. The continual dying of the older hairs, as new hairs develop toward the tip, gives rise to the *migration of root hair zones*, making absorption possible from new soil regions (figs. 4, 5). Most root hairs are ephemeral structures, lasting only a few days or weeks. On tree roots, however, they may endure for several months, while in certain Compositae root hairs two and three years old have been found.



FIGS. 4, 5. — Seedlings of wheat (*Triticum sativum*): 4, a seedling soon after germination; 5, a seedling four weeks older; the root regions, which in 4 are hairclad (*r*) and agglutinated to soil particles, have become hairless in 5 (*r'*), while the younger portions (*r''*) deeper in the soil have hairs; note the hairless root tips; the wheat grain (*g*) remains in the earth, illustrating hypogaean germination (p. 452). — After SACHS.

When unimpeded, root hairs grow at right angles to the root, showing no reaction to gravity stimuli. The hairs become variously gnarled and contorted (fig. 6) through contact with soil particles, with which an intimate cementation is effected by the transformation of the outer layer into mucilage. So close is this attachment that when a plant is pulled from the ground, considerable earth adheres to the root hairs (fig. 1), which are more apt to break than to separate from the soil particles; this indicates the important part played by root hairs in anchorage, especially in seedlings. The adhesion of hairs to

soil particles is of still greater advantage in absorption, since most of the available water surrounds the particles as a film, in which are also most of the salts utilized by plants as food materials. The carbon dioxide excreted by the root hairs assists in dissolving the soil salts.

The influence of external factors upon absorption. — The amount of absorbed water decreases as the soil becomes desiccated, because of the increasing concentration of the soil solutions and because of the increase in the forces by which the thinner water film is held to the surface of the soil particles. Similarly, the absorption of water and solutes is reduced greatly at low temperatures, frozen soils being physiologically as dry as those of deserts. In both dry and frozen soils the root hairs even may exude water instead of absorbing it. Plants differ widely in regard to absorption, some carrying on their activities in spite of the almost perpetually low temperatures of polar soils. High temperatures favor maximum absorption, if the water supply is adequate. Another important factor is the degree of concentration of the medium, strong solutions of sodium chloride and similar salts greatly retarding absorption; probably it is for this reason that salt marsh plants often have an inadequate supply of water.[1] Absorption

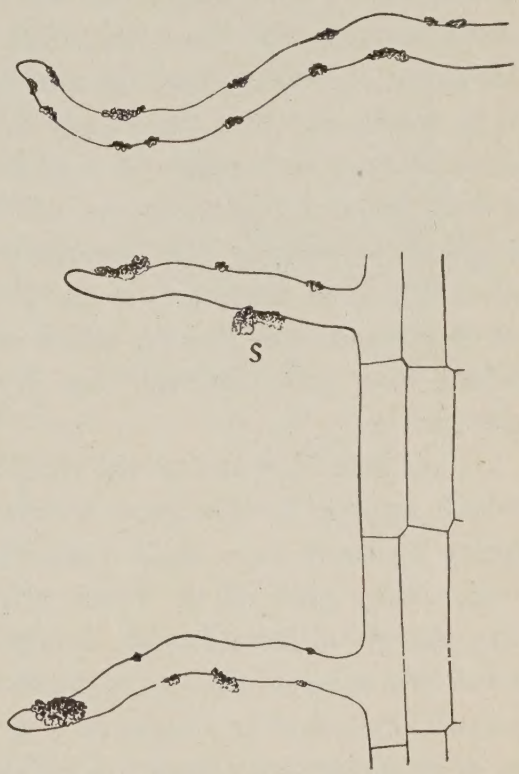


FIG. 6. — Root hairs of a lettuce seedling (*Lactuca sativa*), which have developed in the soil; note that the hairs are somewhat sinuous outgrowths (thus contrasting with air-grown root hairs) from the lower portion (*i.e.* toward the root tip) of the epidermal cells, and that not all epidermal cells give rise to hairs; note also the attached soil particles (*s*); highly magnified.

[1] It is important to note, however, that the osmotic pressure of the cell sap of plants varies widely with the habitat, being least in submersed hydrophytes and greatest in xerophytes and in salt marsh plants. The sap of salt marsh plants may have a pressure of 20–40 atmospheres, as against four or five atmospheres in pond aquatics; hence, the former may be as able to absorb water from a concentrated solution as are the latter from a dilute solution. Many desert plants, especially shrubs, have a pressure of 35–100 atmospheres, and thus are better able than are other plants to utilize the scant water of dry soils.

seems also to be difficult in peat bogs, though the reason is less obvious. Possibly the presence of deleterious substances in the bog water is a factor of importance.

Soil exhaustion and root excretions. — The migration of root hair zones facilitates the invasion of new areas by growing roots. The advantage of such migration often is assumed, it being asserted that roots exhaust the food materials in any given portion of the soil. However, it is likely that the amount of mineral matter used by plants is so small, and that the supply in the soil commonly is so great, that uncultivated soils rarely if ever are exhausted. Furthermore, plants sooner or later return to the soil the mineral matter that they took from it. Probably the " sterility " of many soils is due less to the abstraction of necessary elements by vegetation than to the addition of deleterious substances, which may be definite root excretions, or which may arise through the decomposition of organic material in the soil.

It has been shown that the roots of certain plants excrete substances which impede further root activity. Thus the invasion of new soil areas by roots may make possible their escape from the substances which they give off or which arise by subsequent decay. Even in the case of cultivated crops, it is probable that fertilizers may at times be of less value as sources of plant food than in their action upon soil constituents and in counteracting the noxious effect of root excreta or of decaying vegetation. Certain root enzymes are oxidizing agents of much importance and assist in the destruction of the deleterious soil compounds; however, when these compounds are present in excess, the oxidizing action becomes lessened and the addition of nitrates and of other fertilizer salts is of great value. Farmers have long believed that fields occasionally should lie fallow; the advantage therefrom may be in the facilitation of the oxidation and the removal of deleterious substances. It seems likely that substances given off by plants of a particular species often are more injurious to plants of their own kind than to plants of other species, a fact that may help explain the value of crop rotation.

Variations in the form and the development of root hairs. — Usually, when a seedling is transplanted, the hairs die at once, thus reducing

Furthermore, it has been demonstrated that in the cell sap of various salt water plants, the osmotic pressure varies considerably from time to time, corresponding with similar variations in the medium.

the amount of water admitted. Wilting soon occurs, and it is only when new hairs have grown that the plant revives. Root hairs developed in moist air collapse when brought into a drier medium.

When maize roots are grown in water, hairs commonly are absent, while a vigorous growth, apparently exceeding that in the soil, is obtained in moist-air cultures (fig. 7). The same is true, perhaps, of the majority of plants, but there are many exceptions, as in wheat and oat seedlings, though the latter usually fail to develop hairs in water after the food within the seed is exhausted. Wheat and oat seedlings also have hairless roots in concentrated solutions, probably because the latter inhibit the absorption of the water necessary for hair development.[1] Oxygen is necessary for the development of root hairs, and it may be that their absence or weak development in ponds and swamps is due in part to low oxygen content.

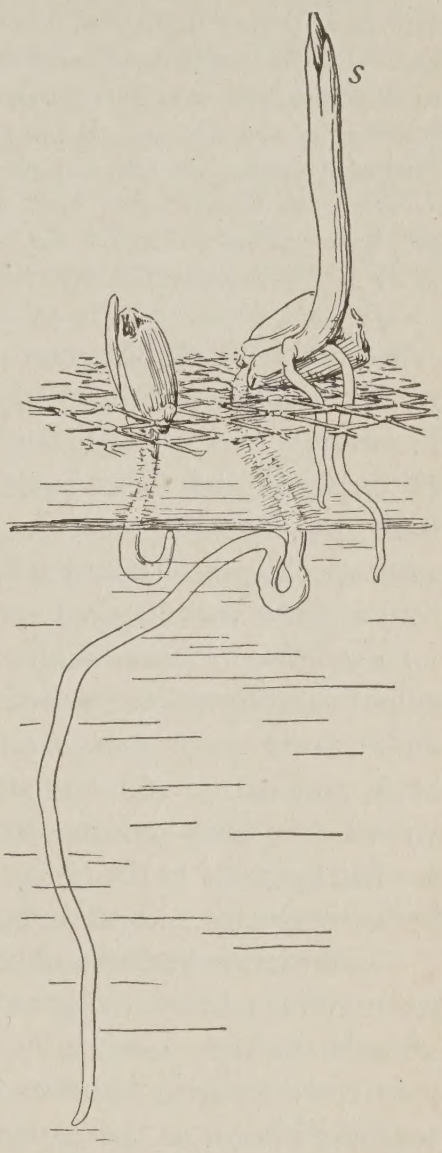


FIG. 7. — Seedlings of maize (*Zea mays*) that have grown in moist air just above water; note that the submersed portions of the roots are hairless and exhibit irregular growth curvatures; the older leaves (*s*) ensheath the delicate younger leaves; maize seedlings illustrate hypogaean germination.

The exact factors that determine root hairs are not certainly known, but they appear to develop best when root growth is retarded, and especially when retardation is differential. When roots elongate rapidly, epidermal cells tend to elongate in the same direction, but when roots elongate slowly, epidermal cells grow transversely, developing into hairs. Root elongation near the tip probably is so rapid that the epidermal cells grow chiefly in a longitudinal direction. A short distance back, cortical elongation ceases, but the epidermal cells, continuing to grow, develop transversely rather than longitudinally. Probably the occurrence of hairs at the root tips of certain xero-

[1] However, some salt marsh plants, such as *Salicornia* and *Zostera*, have an abundance of root hairs, showing that different species react differently to similar stimuli.

phytes is due to slow root growth. Differential growth often leads to the twisting of the root in water cultures, and hairs may occur on the kinked portions.

Maize roots have hairs in water if elongation is mechanically retarded; this may explain why some hairless water roots, as in *Elodea*, develop hairs as soon as they enter the soil (maize roots, however, are hairless in saturated soil). Contact with solid bodies also may favor hair development. High temperatures favor both water entry and root growth, but are detrimental to the development of root hairs, further strengthening the root retardation theory. Sometimes there seems to be a correlation between root hairs and shoots. An irrigated seedling of the creosote bush (*Larrea tridentata*) has ample tops and few root hairs, while the reverse is the case with a plant in dry soil.

Variations in the occurrence of root hairs. — While air roots and water roots commonly are hairless, most soil roots have hairs. Wet soil, as in swamps and beneath ponds, presents a condition transitional between water and mesophytic soil; in such habitats most roots have hairs, but some are hairless. Hairs are more abundant, even in the same species, in soil beneath flowing water than in soil beneath standing water. The root hairs of some xerophytes have rigid lignified walls; for example, in *Pinus edulis* they are stiff and brown. In some succulent xerophytes (as *Opuntia*) hairs occur to the extreme root tip. In most plants whose roots are invested with fungi, such as the conifers, oaks, and many tuberous and bulbous plants, roots hairs are either almost or entirely wanting (fig. 413). The roots of parasites commonly are hairless, and in the green partial parasites all gradations are found between species with abundant hairs and those with none (p. 287).

The structure and rôle of soil roots. — *General features.* — Roots are more uniform in their appearance than are stems and leaves, and there probably is some connection between such uniformity and the comparatively uniform habitats in which roots grow. The root of the seedling, known as the *primary root*, is a *taproot*, being the main descending axis of the plant (fig. 2). At first this root with its hairs represents the entire absorptive and anchorage system. Very soon branches appear, known as *secondary roots*, which differ from stem branches in their irregular position and in their endogenous origin; shortly the root system becomes a most complex affair, owing to repeated branching. In many plants the primary root persists throughout life, continuing to elongate and to grow in diameter; persistent primary roots of this character, which often are taproots as well, are found in the carrot, dandelion, dock, and in many trees (fig. 9). In many other plants, especially in those that reproduce by means of underground stems, the

primary root soon dies, its place being taken by adventitious roots (p. 19). Roots, particularly those of trees and shrubs, are made up largely of woody tissue, which serves as an avenue of conduction to and from the root tips; also, through the stiff cell walls, these tissues give mechanical strength to the roots. Some of these wood cells have relatively capacious cavities and are dominantly conductive, whereas others consist almost wholly of thickened walls and are chiefly mechanical; see detailed discussion of conductive and mechanical tissues, pp. 195 and 211. The penetration of roots into new soil regions takes place without injury to the delicate growing root tip, because the latter is protected by a *root cap*, consisting of older and less delicate cells, which slough off and become slimy, as they are pushed ahead of the elongating tip.

Roots play an important rôle in anchorage and in nutrition. In many species all roots take part in both processes, but there are some plants in which *anchoring* and *nutritive* roots are in sharp contrast. The former have a central vascular strand composed of thick-walled cells of small caliber; nutritive roots, however, have prominent pith and vascular elements that are relatively thin-walled and of large caliber. If growing roots are subjected to tension, they develop into anchoring roots, while roots not so subjected develop into nutritive roots (figs. 38, 39). Many cacti have strong descending anchoring roots and weak horizontal nutritive roots. The root systems of trees differ widely, the ash, for example, having roots of great length, while the more numerous roots of the beech are much shorter and finer.

Roots as anchorage organs. — In a mature plant with a complex root system, a division of labor is manifest. Absorption is limited to the younger portions of the roots, where there is a delicate epidermis permeable to water and salts. Anchorage, on the other hand, is preeminently the rôle of the much-branched root system. On the whole there is a sort of correlation between the developing stems and roots, large aerial stem systems commonly being associated with extensive root systems. Only in certain situations, such as swamps (see p. 25), or when there are unusual winds, as during tornadoes and hurricanes, are tree " windfalls " a common sight The effectiveness of roots as anchorage organs is well displayed along streams and shores, where erosive forces are active. In such situations the earth often is held firmly in place by matted roots and it is only by undermining the grasses and trees, which may even overhang in such places, that the

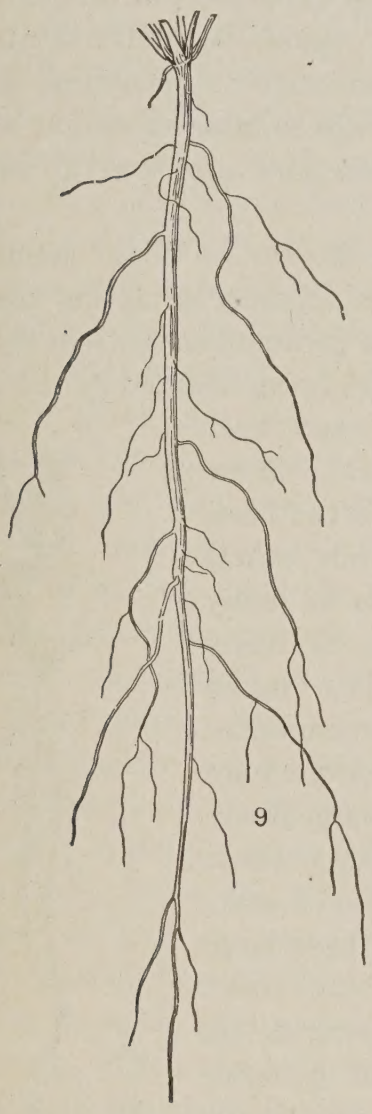
erosive forces are able finally to dislodge the plants and to encroach farther upon the land. Even more striking is the behavior of roots in regions of shifting sands along seacoasts, where many grasses and other plants are able not only to maintain themselves, but even to check the progress of the sand (fig. 8). Such plants are known as *sand binders*, and are of great importance in preventing the encroachment of

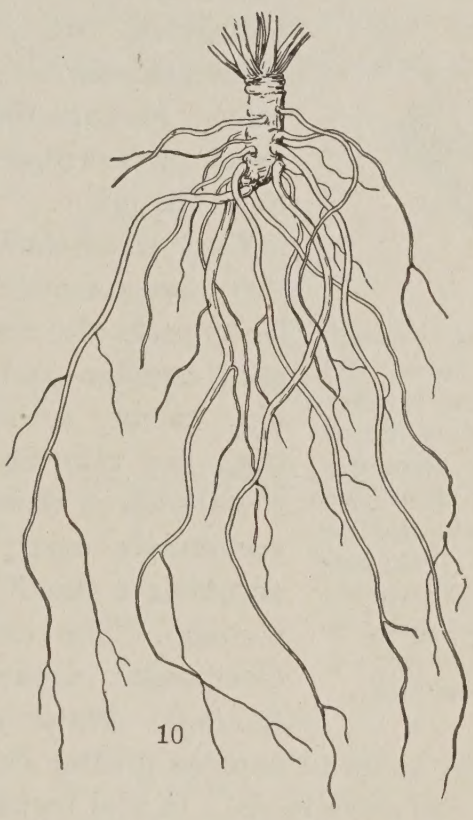
FIG. 8. — A sand-binding grass (*Calamovilfa longifolia*) holding a mound of sand in place by its numerous long and slender but tough roots; to the left are exposed roots and a trough blown out by the wind; note the small herbs among the grass culms, by which they are protected; Dune Park, Indiana. — Photograph supplied by MEYERS.

sand upon villages and farms, even being planted for that purpose in many places.

Gravity and the direction of root growth. — The tendency of roots to grow downward (*i.e.* to exhibit *progeotropism*) makes possible a favorable relation to absorption and anchorage. The geotropic reactions of roots are well shown when seeds germinate on the soil surface; if the root issues from the upper side, it may curve through an arc of 180°, and grow directly down into the soil. But while the taproot usually grows straight down in this fashion, the numerous side roots branch out in

almost all directions. The advantage of such a habit is clear enough, but the cause is obscure. If the growing part of a taproot is removed, some of the stronger side roots commonly begin to grow straight down (figs. 9, 10). Apparently there is something in the taproot which inhibits the expression of progeotropism by the side roots. The removal





FIGS. 9, 10. — Roots of the peppergrass (*Lepidium*): 9, an ordinary primary root with laterals; 10, a root originally similar to 9, but from which vigorous lateral roots have developed, following the removal of the primary root.

of the taproot removes this inhibition and the side roots change their growth direction.

Water and the direction of root growth. — Roots usually grow toward moisture; that is, they are *prohydrotropic*. Water and gravity often combine to cause downward growth in roots, but commonly the water influence is the stronger of the two. When seeds are planted in such a way that the source of water is at one side rather than from beneath,

the roots grow laterally, not vertically (fig. 11). In nature similar phenomena are seen along ditches and irrigation canals and on the sides of vertical cliffs. Prohydrotropic root reactions are of great advantage in view of the dominant rôle of water in the life of plants. Various factors other than water prevent the expression of progeotropic tendencies. In rocky regions, where the strata are horizontal, the roots are unable to penetrate downward. Perhaps the most notable exception to the usual progeotropic reactions are seen in swamp roots (p. 23).

FIG. 11. — A seedling of maize (*Zea mays*) that has been grown at the edge of a funnel whose surface has been kept moist; note that the root is prohydrotropic, following the moistened surface, instead of growing vertically downward.

Food accumulation in roots. — While stems are the most conspicuous food-accumulating organs, fleshy roots also are of great importance in this regard, familiar examples being afforded by the parsnip, carrot, turnip, and beet (fig. 12; also fig. 21). Some roots, such as those of the beet, accumulate sugar, while others accumulate starch (as in many orchids). The roots of many Compositae accumulate inulin (p. 429). Water is accumulated in fleshy roots to an even greater degree than are starch and other foods. In arid regions large fleshy roots are frequent, and sometimes plants whose stems are small and delicate have roots of enormous size. Various species of *Ipomoea* have large roots rich in foods; among these is the sweet potato (*I. batatas*). The man-of-the-earth (*I. pandurata*) has much larger roots, and *I. leptophylla* of the plains has roots that are even gigantic when compared with the relatively small aerial organs.

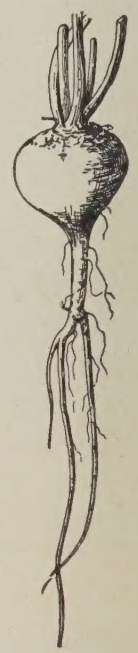


FIG. 12. — A beet (*Beta vulgaris*), illustrating a much enlarged primary root; in such roots large quantities of water and food accumulate.

There appear to be several advantages associated with food accumulation in roots. Such organs seem better protected from animals and from low temperatures than are aerial organs, and unquestionably they are better protected from desiccation. It seems more than a coincidence that

the greatest development of large fleshy roots is in those regions where the danger from drought is the greatest. While the most striking illustrations of fleshy roots are found in arid regions, many plants of our woods and fields, such as the dandelion, dock, evening primrose, and various orchids, have similar roots that accumulate much food and water.

The duration of roots. — The classification of plants into annuals, biennials, and perennials is based chiefly upon the length of life of roots, though many herbs with perennial underground stems have annual roots. The conditions that determine duration are not known, though a little light is thrown on the subject by the behavior of annuals and biennials. A *biennial* is a plant that lives in two vegetative periods, while an *annual* lives in but one. Many plants are annuals or biennials, depending in part upon the time of germination; for example, winter wheat is a biennial, and spring wheat is an annual. Other plants, as the pepper-grass and the shepherd's purse, exhibit similar phenomena. Probably most hardy annuals become biennials if planted in late summer, while many biennials become annuals if planted in early spring, and many more if started yet earlier in a hothouse. When annuals and biennials are grown in uniform conditions, as in the moist tropics or in a moist greenhouse, they become *perennials* in many instances, while certain plants (as the castor bean) that commonly are perennials in uniform climates tend to become annuals in periodic climates. Some annuals (as *Poa annua* and *Senecio vulgaris*) become biennials or perennials when transferred to alpine habitats. In some trees, as the silver poplar, osage orange, and redwood, new shoots arise one after another from the old roots, so that the tree lives long after the first trunk has rotted away. Indeed, so

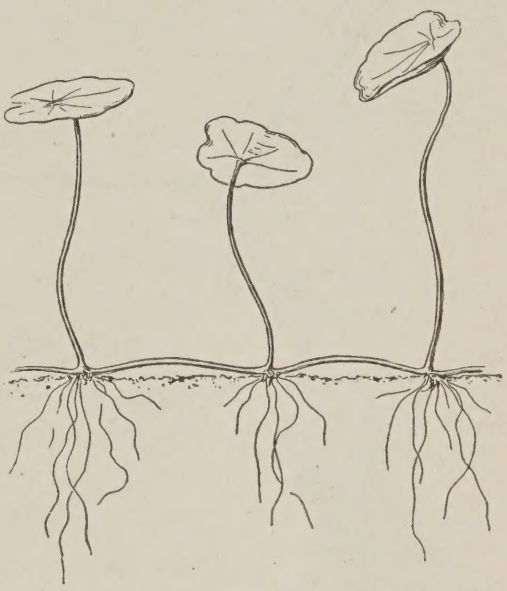


FIG. 13. — A portion of the creeping stem of a water pennywort (*Hydrocotyle*) showing adventitious roots grouped at the nodes, each leaf with its node and group of roots representing a potential plant; the leaves have long petioles, which react readily to changes in the direction of the incident light.

far as root duration is concerned, some perennials may be said to possess a capacity for perpetual life.

The influence of external factors upon root form and development. — *Transplanting in relation to root form.* — Reference has been made to the changed direction assumed by lateral roots when the taproot is removed. The change in the general form of the root system is equally

FIGS. 14, 15. — A branch of the India-rubber tree (*Ficus elastica*), illustrating a method of inducing the development of adventitious roots to facilitate artificial propagation; an incision is made in the stem, which then is wrapped in wet moss (14); shortly, roots develop at the cut surface (15); note the fall of the sheathing stipule (*s*) in 15.

noteworthy, since the large taproot is replaced by a complex of much-branched roots of about equal size (figs. 9, 10). Such a change in form usually occurs when plants (*e.g.* celery or cabbage) are transplanted, since the growing tip of the taproot commonly is destroyed in the process.

Apart from the prevention of overcrowding, transplanting may be of economic advantage, since the shallow and compact root system thus produced is better fitted to utilize commercial fertilizers, which, for the most part, remain in the superficial soil layers; furthermore, the removal of roots from the soil is facilitated.

Nursery trees thrive better than native trees when transplanted, chiefly because a compact root system is developed by frequent transplanting; if a taproot is allowed to grow to a considerable depth, successful transplanting becomes difficult. Such plants as are used for their roots (*e.g.* parsnips and carrots) rarely are transplanted, since the process usually destroys the very parts desired; however, when care is exercised in removing seedlings from the ground, the taproot in some cases continues to grow when transplanted, as in beets. In some plants, as in the radish and the Windsor bean (*Vicia faba*), when the tip is cut just below the region of active growth, the primary root continues its activity, ultimately regenerating a new tip. If the root is cut above this region, further growth is checked and lateral roots take its place, as described above.

Adventitious roots. — *Adventitious roots* (*i.e.* roots arising from stems or leaves) reach their greatest development in plants with horizontal stems (fig. 13; also figs. 286, 291). At first there is in such plants a primary taproot and an erect stem, but soon a horizontal stem develops beneath or just above the surface, whereupon adventitious roots issue from the nodes, and the primary root and stem soon die. In bulbous plants a number of roots of about equal size develop at the base (fig. 299). If such a bulb is removed from the soil at maturity and stored in a dry place, these roots die, but new adventitious roots develop rapidly, when there is access to water.

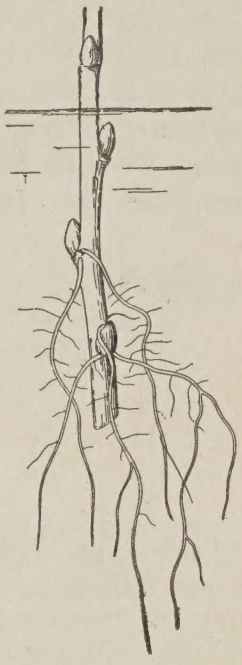


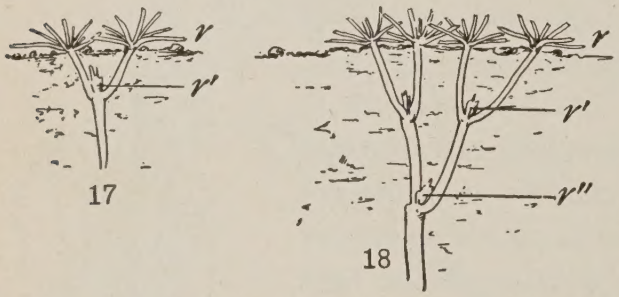
FIG. 16. — A winter shoot of a willow (*Salix*), which has been placed in water; note the adventitious roots that have developed at the nodes.

While adventitious roots usually are observed in plants with runners or with underground stems, many other plants are able to develop such roots upon occasion. When long stems of the black raspberry bend over until they touch the ground, adventitious roots develop; this habit is made use of in artificial propagation, since a new shoot develops where the stem strikes root. The same principle is utilized in the artificial propagation of the rubber plant (figs. 14, 15). If wet moss is tied about a stem, root development at that point is soon incited, whereupon the stem is cut off below the moss and placed in soil.[1]

[1] A remarkable development of adventitious roots is seen on the trunks of some tree ferns (as *Dicksonia*), where they may appear in such abundance as to enclose the trunk in a spongy mass.

Various swamp plants, such as the reed and the swamp loosestrife (*Decodon verticillatus*), strike root where the stem comes in contact with wet soil, and the stems of various willows and dogwoods (as *Cornus stolonifera*) develop roots in abundance when placed in water or in moist soil (fig. 16). Such behavior is of immense advantage in the case of plants that are partly buried by accumulating humus or sand, for as fast as the stems are buried, new adventitious roots appear at higher levels, supplementing the original root system. Some stems, such as those of pines and oaks, are unable to develop roots in this manner, a fact that may account for the early death of these trees when partly buried, in contrast with the phenomenal success of poplars and willows under similar conditions.

Adventitious roots occur less frequently on leaves than on stems. The walking fern (*Camptosorus rhizophyllus*) strikes root at the leaf tip, much as does the raspberry at the stem tip, and in a similar way gives rise to a new plant. While not particularly common in nature, leaf roots are induced readily in a number of species when the leaves are removed from the parent plant and placed in contact with moist soil. In this way gardeners propagate various plants, such as *Begonia*, *Peperomia*, and *Sansevieria* (figs. 239, 240).



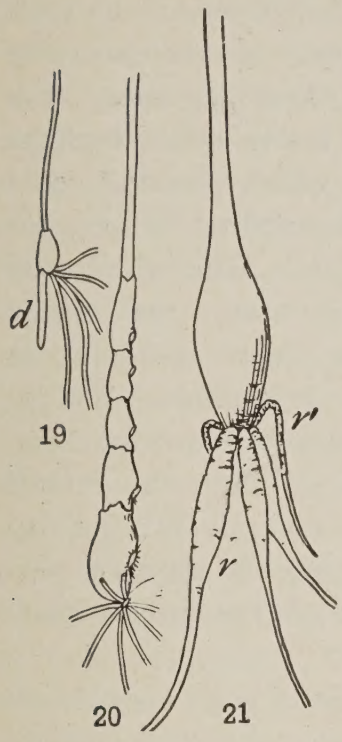
FIGS. 17, 18. — Diagrammatic soil sections, illustrating the lowering of a rosette plant (*Arabis lyrata*) from year to year by root contraction: 17, a two-year-old plant with rosette leaves (*r*) at the surface, and with remains of the previous rosette (*r'*) deeper down; 18, a three-year-old plant, which has remains of a rosette two years old (*r''*), now deeply buried; these diagrams also illustrate multicipital stems.

Probably moisture is the chief factor determining the development of adventitious roots, not alone in water, but also in soil, and in instances like those noted in the rubber plant and in the tree ferns. However, given equal moisture, adventitious roots appear to develop most on darkened and on under surfaces (fig. 239); probably contact with solid bodies also is an important stimulative factor.

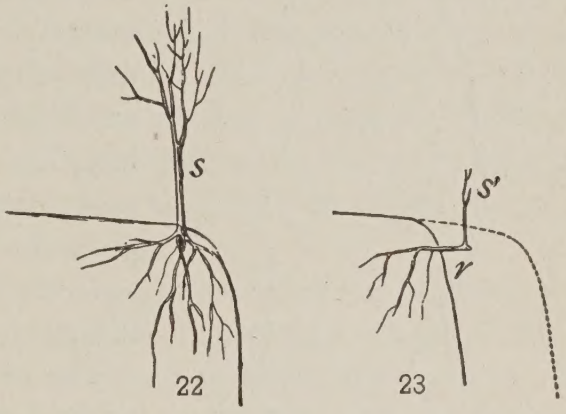
Root contraction. — When a " stemless " rosette plant, as the rock cress or dandelion, grows in a crevice, the position of the rosette in relation to the surface is year by year the same (figs. 17, 18). The very short stem elongates slightly each year, and the root pulls the plant by that much into the soil, so that the rosette remains at a constant level. This phenomenon is called *root contraction;* the mechanism of the process is not fully understood, but its advantage to the plant is very evident. Sometimes the contractile region of the root becomes less than two thirds its original length (the shortening may exceed fifteen millimeters in *Arisaema dracontium*); after contraction the root exhibits transverse folds, and observation shows that the contractile tissue is chiefly the cortical parenchyma (fig. 21).

In white clover and in similar plants, erect or ascending stems are pulled down by the adventitious roots, which develop at the nodes and hold the stems tightly to the soil. The varying soil levels which characterize underground stems of different species often are reached through stem activities (see figs. 19, 20). As crevice roots grow in diameter, the pressure often becomes sufficient to shatter rocks, so that plants contribute materially to rock disintegration.

Propagation by roots. — As a rule, roots do not give rise to buds, nor do they bear stems and leaves. In some plants, notably the silver poplar and the osage orange, stems develop habitually from ordinary soil roots, resulting in a spreading colony of young trees around the parent tree. Many trees and shrubs, especially various poplars and willows, manifest this phenomenon to a marked degree, if the roots are exposed to the air. In the hawthorn, cottonwood, beet, dandelion, and many other plants, roots can be induced to develop shoots, if the entire stem system is removed and the roots are exposed to air and light (figs. 22, 23). The exact factors that stimulate stem growth in these rather unusual conditions are not known. Near the growing point within the root of *Habenaria michauxii* there is organized a bud that later develops into an underground stem.



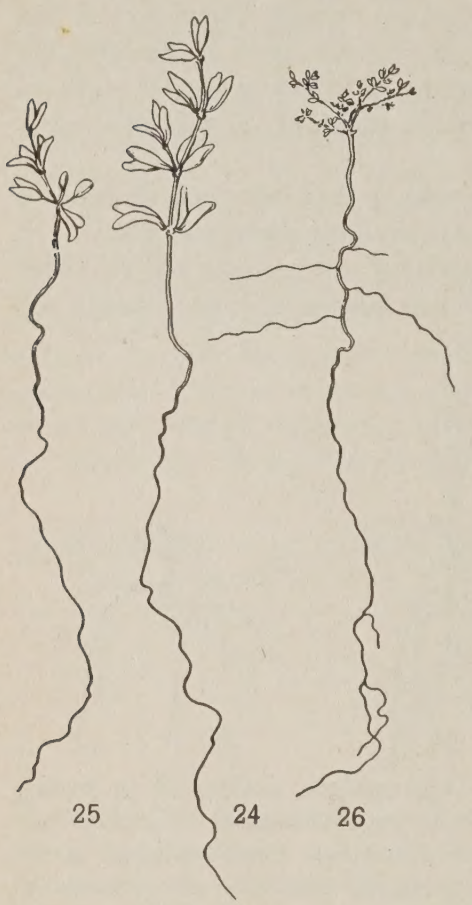
FIGS. 19, 20, 21. — The descent of roots and rhizomes in the soil: 19, a young individual of *Erythronium mesachoreum*, showing a descending rhizome or "dropper" (*d*, see p. 195); 20, an older descending individual, showing remnants of the five preceding years; note the increasing size of the bulb each year; 21, an individual of *Zygadenus tremonti*, illustrating descent by root contraction; note the contractile roots of the current (*r*) and the preceding (*r'*) years. — From RIMBACH.



FIGS. 22, 23. — Diagrammatic sections of an eroding clay bluff, illustrating the development of shoots from roots: 22 represents a hawthorn tree (*Crataegus*) at the edge of the bluff, *s* being the original trunk; subsequent erosion (23) has caused the destruction of the trunk and the exposure to the air of a root (*r*), which has given rise to a new shoot (*s'*).

Water and root form. — The roots of desert plants, as a rule, are extensively developed, at least in comparison with the shoots (figs. 24–

26). Some plants have long and slender roots that reach to great depths or that have considerable lateral extension. In other cases roots of immense size are formed. In alpine regions there are dwarfed shoots associated with roots of ordinary size (fig. 176), and there are many such plants in dry sandy soil. Perhaps the ease with which growing roots penetrate sand accounts in part for their great length. While the initial root system of most trees seems scarcely plastic, later development may vary with the habitat. For example, in swamps the red maple soon loses its taproot, while the lateral roots develop extensively; in dry grounds, however, the taproot persists and most of the lateral roots disappear.



FIGS. 24, 25, 26. — Seedlings of the creosote bush (*Larrea tridentata*), illustrating variations in relative root development in a desert plant: 24 is a seedling grown with an excess of water and showing luxuriant shoot development; 25 was grown with an under-supply of water, and shows a reduced root system and a shoot yet more reduced; 26 is a natural seedling from the desert and shows a much greater root development in proportion to the shoot; all show a strong development of the primary root with but slight development of laterals; 26 is drawn on a much smaller scale than are 24 and 25. — After SPALDING (drawn from a photographic reproduction).

The advantage of great root development in xerophytes is clear enough, since the more extensive the root system, the greater is the area of absorptive surface and the greater the likelihood of root contact with remote supplies of water. The advantage of short roots to swamp plants is not clear; indeed, short roots often fail to afford adequate anchorage, though they may be sufficient for absorption. The advantages of long roots to xerophytes are so obvious that often they have been regarded as sufficiently explained thereby; such an assumption fails to recognize that plants cannot adapt themselves, but must react to the stimuli which influence them (p. 465). If such reactions happen to be favorable, the plant thrives, but unfavorable reactions result in injury or in death.

Our experimental knowledge of roots is not yet sufficient to enable us to explain all their variations of form and size. In the first place it is not certain that the roots of xerophytes actually are longer than those of other plants, though that claim is often made. The optimum development of roots has been shown to occur in soil with a relatively low water content, provided there is enough moisture for good growth. In such relatively dry soil there is a greatly increased absorbing surface and a much greater development of lateral roots and branches than in the same soil with a higher water content. The length of the main roots, however, is often about the same in the dry and in the moist soil. It may be stated with certainty that the roots of xerophytes, as compared with those of mesophytes, are reduced much less than are the shoots, a phenomenon that is not especially difficult to understand. In arid regions the aerial organs of plants are subject to excessive transpiration, a process that retards growth to an amazing extent; the roots of desert plants, on the other hand, are relatively free from the inhibitory influence of transpiration.

Whatever may be true of roots in dry soils, there is no doubt that roots in swampy and boggy soils are short, not only as compared with the shoots, but actually short, as compared with the roots in other habitats. The meager development of bog roots may be explained by the lack of oxygen and by the toxicity and acidity of bog waters. In swamp and bog soils there is relatively little oxygen and growth is known to be inhibited by lack of this element. In such soils the water table is usually near the surface and taproots often die as they reach the water surface and are replaced by horizontal laterals. When the roots are all vertical they, too, often die at the water surface.

If further study should show that generally the roots of xerophytes are not only relatively but absolutely more extensive than are those of mesophytes, it is not to be concluded, in the face of opposing experimental data, that long roots are a reaction to arid soils. It is possible that such xerophytes are by inheritance long-rooted. If a hemlock and a red cedar are grown side by side in similar conditions, the former has a meager and the latter an extensive root system. In the course of evolution short- and long-rooted species are likely to have originated in deserts; of these the long-rooted forms are the more likely to have survived the arid conditions. Similarly both short- and long-rooted forms are likely to have originated in mesophytic habitats, where survival is less a matter of the root system than of stem and foliage characteristics.

Obviously much further experiment is necessary before we may know to what extent root variations are reactions to environment, and to what extent they are congenital or characteristic of the species.

In some cases roots grow directly upward, as in certain palms and mangroves and in *Jussiaea*, or there are erect projections from horizontal roots (known as *knees*), as in the bald cypress (fig. 27). The exact cause of these reactions is not known, but it is probable that the

FIG. 27. — A cypress swamp at low water; note the erect growths (knees) from the roots of the bald cypress (*Taxodium*) and the buttressed bases of the trunks; intermingled with the cypress (the large trees in the foreground with bark shredding vertically) are specimens of tupelo (*Nyssa aquatica;* small trees in the background); Paragould, Arkansas. — Photograph by MEYERS.

small percentage of oxygen in swamp waters and the accumulation of deleterious root excretions and products of decaying vegetation influence the direction as well as the length of roots. It is likely that the inhibitory influence of these factors increases with the depth; the greater amount of oxygen in the surface layers may facilitate growth, in part directly, and in part indirectly, through the partial destruction of deleterious organic compounds by oxidation.

In a stagnant swamp the surface layer is the only place where at the same time water and oxygen are available for root activity, hence it would seem that horizontal roots are best fitted to thrive in such habitats. The explanation of such erect

roots or root branches as those of the bald cypress and of the mangroves is difficult. The erect growth certainly is a reaction to some condition in the swamp, since knees do not develop when the bald cypress is cultivated in uplands. Oddly enough, knees do not develop in deep water, but only in shallow water or in swamps. If these peculiar structures are regarded as reactions to a slight oxygen content, it is difficult to account for their absence in deep water, unless it be supposed that the life conditions there are too poor to permit of growth. The erect roots of *Jussiaea* are spongy structures resembling aerenchyma (p. 68), and they arise from stems instead of from roots; possibly, like aerenchyma, they develop where transpiration is checked.

Much has been said concerning the advantage of cypress knees and of horizontal swamp roots, the prevalent view being that respiration is facilitated by these structures. The efficiency of cypress knees as aerating organs is not known; although their tissues are rather loose, the knees are covered with bark, and often are clothed with dense layers of mosses and liverworts, which must retard the penetration of gases. Furthermore, knees are absent in deep water, where aeration is most needed. The shallow horizontal root system of the tamarack seems disadvantageous in part, since it does not afford adequate anchorage; severe storms may overturn these trees in considerable numbers. Probably horizontal surface roots in swamps are of real advantage in facilitating aeration, though this view is based upon assumption rather than upon experiment.

The *plank roots* of tropical trees, resembling boards on edge, are due to excessive growth on the upper sides of soil roots; the causative factors are unknown, but it is possible that growth is freer in the air than in the soil. An analogous phenomenon, due chiefly to stem activity, is seen in various swamp trees, as the tupelo and the bald cypress, and to some extent in the elm, the base of the trunk being greatly enlarged (fig. 27). Possibly enlarged *buttressed trunks* and plank roots are of advantage in holding trees in place where the soil roots are relatively inefficient as anchorage organs.

Correlation of roots and leaves. — The ecological behavior of a plant cannot be determined from one set of organs. For example, the hemlock and the red cedar have somewhat similar leaves, being small, thick-skinned, and apparently fitted to withstand excessive transpiration. But while the red cedar can thrive in very xerophytic situations, the hemlock thrives best in mesophytic woods with such large-leaved trees as the sugar maple. It is believed that the differing habitats of these two trees is a matter of correlation between roots and leaves, the red cedar having an extensive root system and the hemlock one that is more meagerly developed. It would appear that the ratio between absorption and transpiration determines the habitat for which a plant is fit. It should be emphasized, however, that the lack of experimental evidence makes this theory of correlation as yet merely a plausible hypothesis (see also p. 262).

2. WATER AND AIR ROOTS; RHIZOIDS

Water roots. — The most representative water roots are found in plants that are not attached to a substratum, such as the duckweeds (fig. 28) and the water hyacinth. Such roots are not numerous nor

large, and in most cases branches are few and root hairs wanting; in some duckweeds there is but a single small root to a plant. Thus the modifications induced when soil roots are grown in water (*viz.* reduction in size and in hair production) are seen to be the usual features in aquatic roots. The cause of reduction and of hairlessness in water roots is unknown, though it is likely that the conclusions reached in the case of soil roots are applicable here.

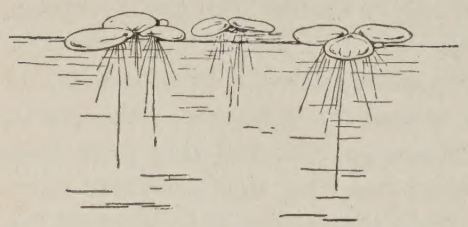


FIG. 28. — Plants of a duckweed (*Spirodela polyrhiza*) floating free on the water, showing flat thalloid shoots, from each of which there depend several water roots. Each thallus or frond represents a single individual that has arisen from another such frond vegetatively; the mother and the daughter fronds remain attached for a time in colonies.

In some water plants, as *Ceratophyllum*, *Utricularia*, and *Salvinia* (fig. 203), roots are wanting and absorption is confined to the leaves and stems. The duckweeds may have several roots (as in *Spirodela*), one root (as in *Lemna*), or no root (as in *Wolffia*); in all three there is a thallus rather than a leafy stem. In the duckweeds absorption is largely through the thallus and in *Wolffia* entirely so.

In water roots the outer layers do not become impermeable with age, so that absorption takes place through the entire surface instead of through the tips only, as in soil roots. Water roots are of no value as anchorage organs, but they may assist in the maintenance of equilibrium. Many aquatic roots contain chlorophyll, and it may be that food manufacture is an accessory rôle of some importance. An interesting feature of water roots is the *root pocket*, a structure that fits over the root tip like a glove finger (fig. 29). Although root pockets are much more conspicuous than are the root caps of soil roots, their advantage to the plant is less evident. Roots intermediate between soil and water roots are found in various attached aquatics, such as *Elodea* and *Myriophyllum*. Horizontal branches give rise to hairless unbranched roots resembling water roots, but, as soon as they enter the soil, they branch freely and produce hairs.

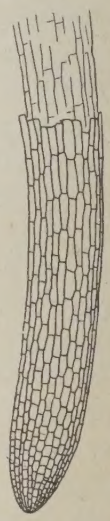


FIG. 29. — The tip of a water root of a water hyacinth (*Eichhornia speciosa*), showing the root pocket, which fits over the root like a glove finger; considerably magnified.

Absorptive air roots. — *Structural features.* — Many plants (known as *epiphytes*) grow on the branches of trees, where the conditions for absorption are much poorer than in the soil. In many tropical orchids and aroids (Araceae), the aerial roots possess specialized absorptive organs (fig. 30). These roots often are silvery white except for the greenish tips, and their most distinctive feature is the outermost or epidermal layer, known as the *velamen*,

which usually is a number of cells thick (fig. 31). At maturity the cells are dead and the walls are variously thickened by reticulated or spirally arranged fibers (fig. 32). The outermost cortical layer, the *exodermis*, occurs beneath the velamen as a sheath of cells with walls strongly thickened by cutin or cork. Some cells in this layer, known as *transfusion cells*, remain with relatively unthickened walls and are said to serve as passageways for water from the velamen to the cortex (fig. 33). The cortical cells resemble those in soil roots, except that they contain an abundance of chlorophyll, which accounts for the greenness of the roots when wet (fig. 34).

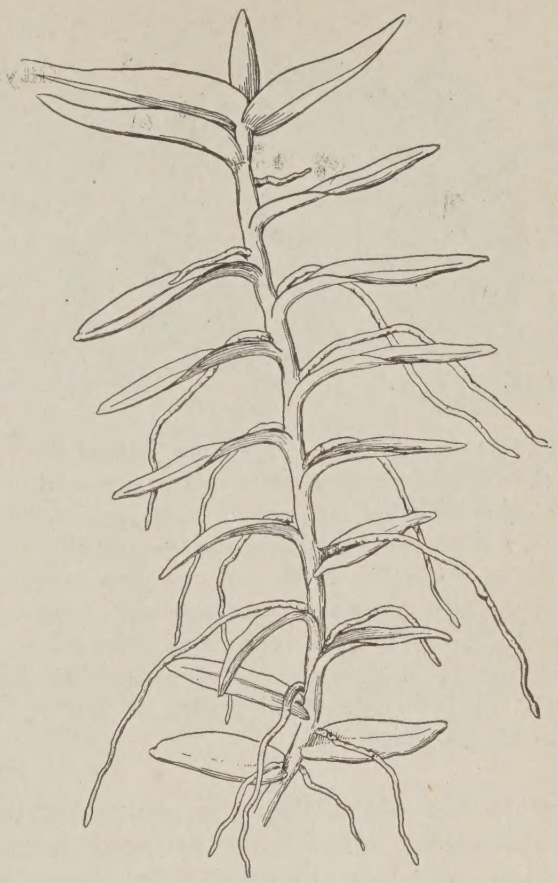


FIG. 30. — A tropical epiphytic orchid (*Epidendrum ramosum*), showing aerial absorptive roots arising adventitiously from the nodes, and mostly just above the leaves, which exhibit distichous phyllotaxy (*i.e.* with leaves alternating in two vertical rows, p. 65).

Rôle. — Water can be taken up with rapidity by the velamen when dry, the process being a capillary phenomenon and comparable to the absorption of water by blotting paper, and quite unlike absorption by root hairs. On the other hand, the passage of water and salts from the velamen through the transfusion cells to the cortex is a slow osmotic process quite comparable to absorption by root hairs. The velamen is an organ of water accumulation as well as an organ of absorption, and it retains water for hours and even for

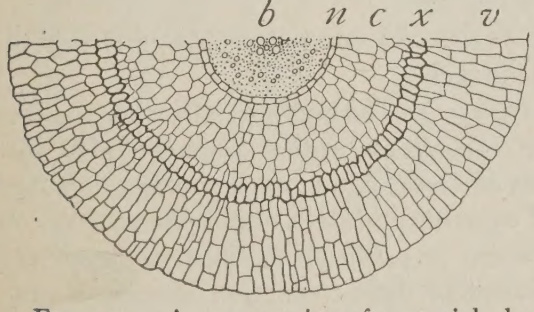
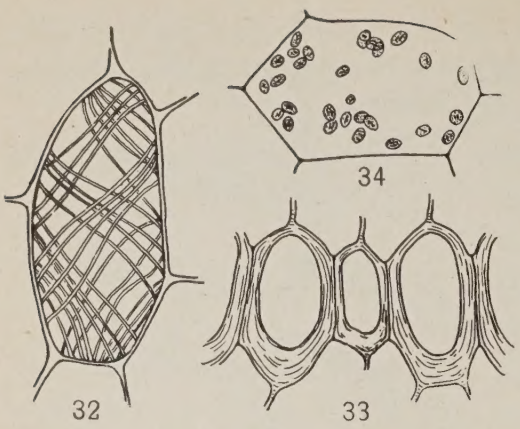


FIG. 31. — A cross section of an aerial absorptive root of a tropical epiphytic orchid, showing the velamen (*v*), the exodermis or outermost cortical layer (*x*), the main body of the cortex (*c*), the endodermis or innermost layer of the cortex (*n*), and the conductive region (*b*). The velamen (*v*) represents the epidermis, and is composed of dead cells, which, when dry, absorb water with great rapidity; considerably magnified.



FIGS. 32, 33, 34. — Cells from various regions of an aerial absorptive root of a tropical epiphytic orchid, as seen in cross section: 32, a velamen cell, showing the characteristic fibrous thickening of the wall; 33, three exodermis cells, showing considerable wall thickening, especially toward the cortex (lower side in figure); 34, a cortical cell, showing chloroplasts with included starch grains; all figures highly magnified.

days. Its significance is still more obvious when it is realized that only liquid water can be utilized by plants; orchids even decrease in weight in moist chambers unless watered. Hence it is not surprising that epiphytes with absorptive roots are confined to warm and humid climates, where rain or dew is almost continually available.

The chlorophyll which is present in air roots probably is of some importance in food manufacture. Doubtless the presence of chlorophyll in these organs is related to light, since various soil roots develop chlorophyll when exposed to it. In *Taeniophyllum* and in similar orchids with greatly reduced stems and leaves, the roots, which are the chief food-making organs, are flattened rather than round, and lack the usual radial structure. The lighted side has a thick-walled exodermis and prominent cortical chlorophyll but little or no velamen, while the shaded side has a strong velamen, a thin-walled exodermis, and abundant root hairs (fig. 35). Absorptive air roots play only a small part in anchorage, though in some cases, especially in the flattened roots just cited, they adhere closely to the tree branches.

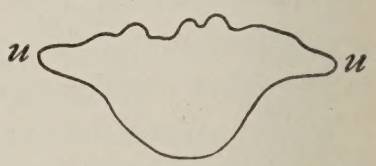


FIG. 35. — An outline, as seen in cross section, of a dorsiventral orchid root (*Aeranthus fasciola*), showing the expanded upper portion (*u*), which contains most of the chlorophyll. — After JANCZEWSKI.

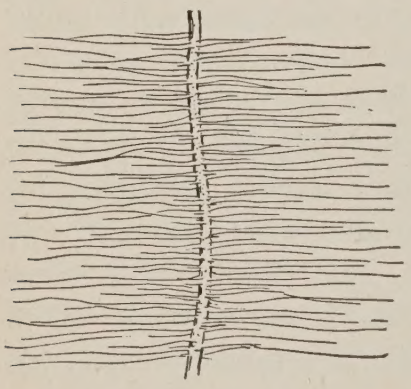


FIG. 36. — A portion of a progeotropic rhizophore of *Selaginella apus*, densely clothed with horizontal root hairs, as a result of growth in a moist chamber; considerably magnified.

Variations. — The high specialization and the obvious rôle of absorptive air roots give the question of their origin much interest, but the lack of experimental data makes the solution of the problem very difficult. The most characteristic feature of these roots, the velamen, is possessed by nearly all aerial roots and by almost no soil roots, except in a few forms, such as *Bletia* and *Spiranthes cernua;* thus the medium seems to have a rather definite relation to the formation of the velamen. The most obvious

reaction of air roots to changed conditions is in hair production. Most air roots are hairless; some (as in species of *Anthurium*) commonly possess hairs, and root hairs develop in a number of species when the roots are exposed to unusually moist air (fig. 36). A curious exception to the usual kind of root hair is found in some air roots, where the hairs are stiff and rigid structures of long duration.

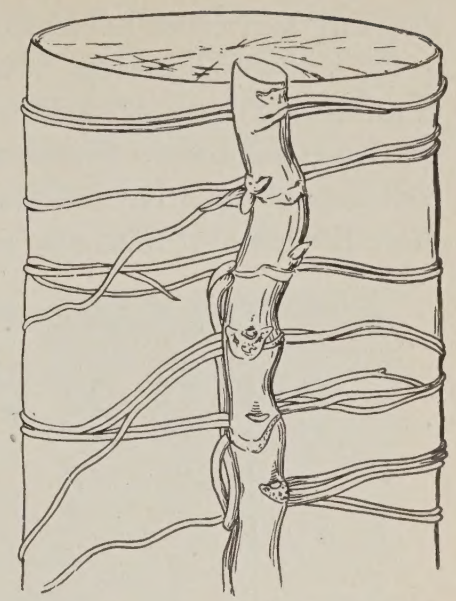
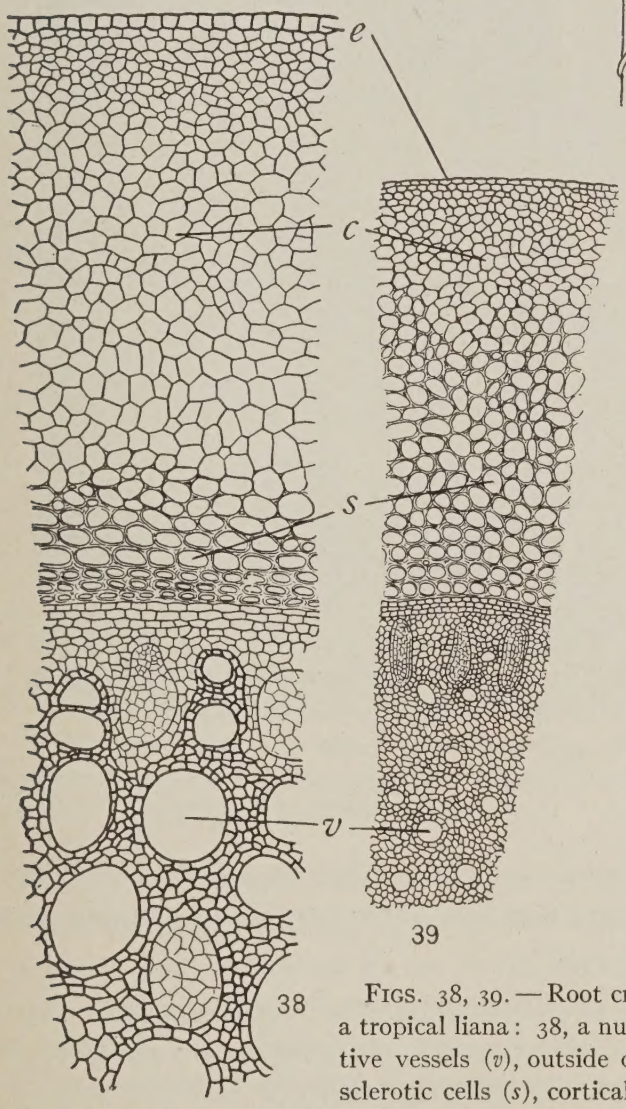


FIG. 37. — A portion of the stem of a liana (*Philodendron melanochrysum*) with horizontal adventitious roots clasping the trunk of a tree (*Canarium*), thus serving to anchor the liana to its support. — From WENT.

Anchoring air roots. — Some climbing plants, as poison ivy and English ivy, are anchored to the supporting trees by adventitious roots, which clasp the trunk or penetrate into bark furrows. Such roots grow horizontally rather than downward (fig. 37), notably in certain tropical climbers, whose roots are as sensitive to contact stimuli as are many tendrils. If these roots are at all geotropic, the bark



FIGS. 38, 39. — Root cross sections of *Philodendron lacerum*, a tropical liana: 38, a nutritive root with many large conductive vessels (*v*), outside of which is a sheath of thick-walled sclerotic cells (*s*), cortical parenchyma (*c*), and epidermis (*e*); 39, an anchoring root with much smaller vessels (*v*) and with a much thicker sclerotic sheath (*s*); the nutritive root is much the larger, the two figures being equally magnified. — From WENT.

moisture and other influences are sufficient to overcome gravity and to induce lateral growth. Climbing roots commonly are supposed to be anchoring roots only and not absorptive, since the plants also possess nutritive soil roots; these two kinds of roots exhibit the structural contrasts of nutritive and anchoring soil roots, but the differences are more pronounced (figs. 38, 39). In the English ivy the anchor roots

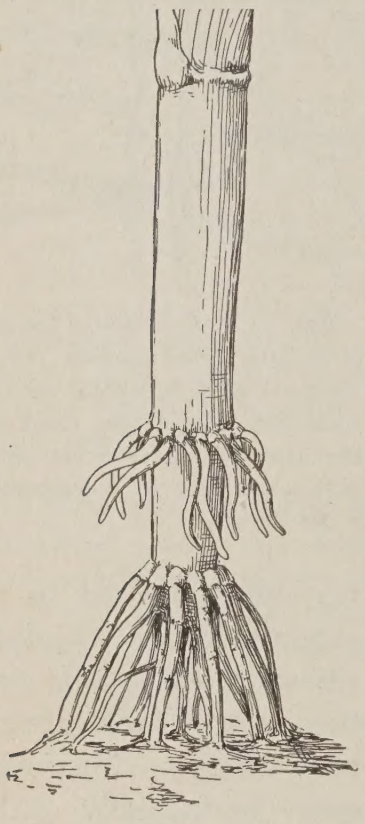


FIG. 40. — The basal portion of a maize stalk (*Zea mays*), showing prop roots arising from the lower nodes; note that the stalk becomes thicker upwards.

FIG. 41. — A strangling fig (*Ficus*) that began life as an epiphyte, but which now has absorptive ground roots, as well as roots that envelop the tree (*Bischofia trifoliata*) on which the fig started; Lamao Forest Reserve, Philippine Islands. — From WHITFORD (Courtesy of the Philippine Bureau of Forestry).

resemble ordinary adventitious roots in a state of arrested development, and they become transformed into such roots upon coming into contact with moist earth.

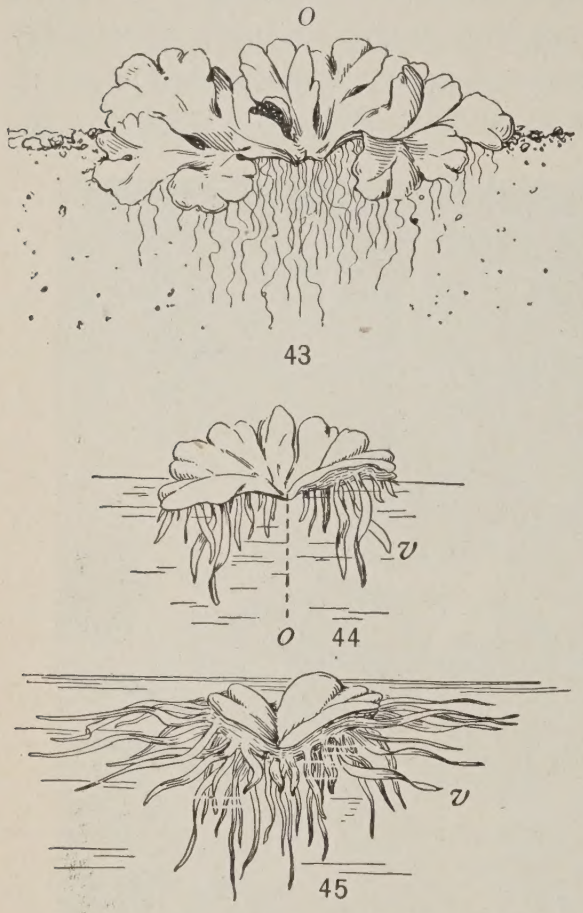
Most epiphytes are anchored to the substratum by roots that may or may not be absorptive. For example, many species of *Tillandsia* are anchored to branches by wiry roots that absorb little or nothing from the bark, the leaves being the chief absorptive organs (p. 130). Various ferns thrive equally well in the ground or on trees, but in the latter case they are anchored by ordinary absorptive roots.

Prop roots. — In various monocotyls, such as the screw pine (*Pandanus*), Indian corn, and certain palms, roots issue from the stem at various levels, and grow obliquely downward into the soil; in the air they are relatively unbranched, but they branch profusely upon striking the soil (fig. 40). Since monocotyls possess but a limited power of diametral growth, a tree like the screw pine develops a top-heavy in-

FIG. 42. — The interior of a mangrove swamp, showing the prop roots of *Rhizophora mangle* together with arched roots that make a labyrinthine tangle near the ground; Miami, Florida. — Photograph by E. W. COWLES.

verted cone instead of a stable cone, as in dicotyls, so that its prop roots are of great advantage in preserving equilibrium. In the banyan and in other species of *Ficus*, roots issue from the horizontal branches and grow directly downward to the ground. The support given by such roots makes possible the enormous spread of the banyan. Many species of *Ficus* (sometimes called strangling figs) usually begin life as epiphytes, some of the roots developing in the dead bark and others descending along the trunk to the ground. After a time all of the nour-

ishment comes from the ground, and the supporting tree is likely to be strangled by an anastomosing network of enveloping roots or borne down by the weight of the growing *Ficus* (fig. 41).



FIGS. 43, 44, 45. — Plants of a liverwort, *Riccia;* 43, an individual grown with soil contact and showing a luxuriant but thin and much-lobed thallus and an abundant growth of rhizoids (*r*); 44, a portion of the individual figured in 43, transferred to water, and allowed to develop there for some weeks; 45, the plant figured in 44 at a later stage; note that in 44 and 45 the thallus is much smaller and thicker than in 43, and that flat ventral scales (*v*) have taken the place of rhizoids (*r*); through the death of the old part of the thallus (*o*) the new lobes become detached at the sinuses, resulting in the vegetative origin of a number of individuals from one; all figures somewhat magnified.

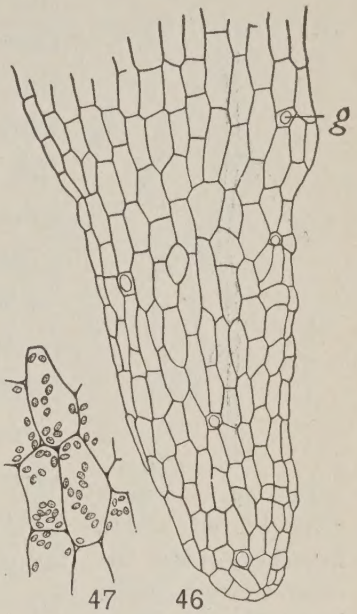
In Washington and in British Columbia the hemlock often germinates on stumps, logs, or standing trees, and has a subsequent history somewhat comparable to that of *Ficus* in the tropics.

The banyan habit is illustrated on a small scale by *Selaginella*, especially in moist chamber cultures, where there develop *rhizophores* with numerous root hairs (figs. 36, 202). In the mangrove, roots are put forth much as in *Ficus*, but they branch profusely in the air and spread out laterally (fig. 42). So abundant are these roots in mangrove swamps that they form a dense network over the soil, and are of much importance in supporting the numerous branches, owing to the early death of the basal part of the primary trunk. The factors operative in the production of prop roots are quite obscure; in *Selaginella*, water seems to be an important stimulus.

Liverwort and fern rhizoids. — *Structure.* — The *rhizoids* of liverworts and of fern prothallia commonly are colorless, unicellular outgrowths of special external cells, and may or may not eventually be cut off therefrom by a cell wall (fig. 43). They closely resemble root hairs in structure, but usually they are of much greater length and their protoplasm is more thinly disseminated. In the Marchantiaceae, rhizoids are of two kinds, *plane rhizoids* as above described and *peg rhizoids*,

in which the cell wall grows out internally into peglike or antlerlike projections. The plane rhizoids occur chiefly on the younger apical and midrib portions, while the peg rhizoids occur on the older marginal portions.

Reactions to external conditions. — Rhizoids are progeotropic, prohydrotropic, and apophototropic, thus agreeing with roots and differing greatly from root hairs. In *Marchantia* gemmae or fern prothallia, rhizoids may be induced at will on either side of the thallus by exposure to the proper stimuli (moisture, darkness, contact, etc.); after the rhizoids appear, their growth direction may be altered by altering their relation to light, moisture, or gravity. Rhizoids are, however, more responsive to moisture than to other stimuli.



FIGS. 46, 47. — A ventral scale from the water form of *Riccia:* 46, the tip of the scale, showing scattered mucilage cells (*g*); 47, a few of the scale cells, showing chloroplasts; both figures highly magnified.

FIG. 48. — A moss plant (gametophyte), showing the aerial stem (*s*) with leaves (*l*) in several vertical rows; the underground organs are branched structures, the rhizoids (*r*).

When *Lunularia* is grown in solutions deficient in nitrogen or in phosphorus, the rhizoids become greatly elongated, while the thallus is poorly developed. No rhizoids develop on *Lunularia* in pure water, but enough salts are dissolved from ordinary laboratory vessels to induce rhizoids abundantly. Very plastic liverworts are *Riccia natans* and *R. lutescens*, plants that grow either in soil or in water. Ordinary rhizoids develop in the soil (fig. 43), but in the water their place is taken by large and conspicuous *ventral scales* (figs. 44–47). Rhizoids, like root hairs, are better developed in xerophytic than in hydrophytic forms, and aquatic species (as *Riccia fluitans*) commonly are without them.

Rôle. — Liverwort and fern rhizoids obviously are anchorage organs, and generally they are believed to be organs of absorption also, although the proof therefor is not so conclusive as in the case of root hairs. Since the thallus is close to the ground and permeable, rhizoid

absorption may be of minor value. The arguments for the absorptive rôle are (1) cementation to soil particles (fig. 382) and modification in rhizoid form as in root hairs, and (2) the observed rise of colored fluids and the crystallization within the rhizoids of the Marchantiaceae of absorbed salts (as Berlin blue). The special advantage of the peg rhizoids, though much discussed, is not known.

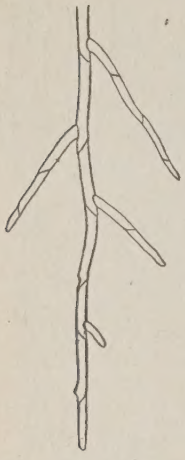
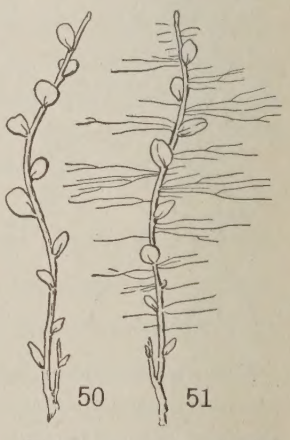


FIG. 49. — A moss rhizoid with its branches; note the oblique cross walls, immediately above which branch rhizoids originate at a definite position; highly magnified.

Moss rhizoids. — *Structure and habitat variation.* — Moss rhizoids commonly are brownish, branched, multicellular cell filaments with oblique cross walls. Often they have a rootlike aspect, by reason of a strong central trunk with small lateral branches (figs. 48, 49). Some mosses (as *Funaria*) develop very long rhizoids in solutions deficient in nitrogen or phosphorus. Rhizoids develop abundantly on the aerial stems of some mosses (as *Thuidium*) when grown in a moist atmosphere; such rhizoids are as brown as those developed in the soil in spite of the exposure to light (figs. 50, 51). Rhizoids are developed abundantly also in xerophytic mosses, and sometimes in mosses that frequent running waters, while they are poorly developed or wanting in pond and swamp mosses. In dry soil *Polytrichum juniperinum* exhibits a vigorous development of soil rhizoids, but in swamps these are largely replaced by aerial rhizoids (" stem felts "). Usually rhizoids are better developed in erect mosses which have prominent " vascular " tracts, and which grow somewhat separately (as *Polytrichum*, *Catharinea*, and *Mnium*) than in mosses without such tracts, which grow in dense cushions or mats (as *Leucobryum*, and *Sphagnum*, which has no rhizoids).



FIGS. 50, 51. — Aerial rhizoids: 50, a swamp moss as ordinarily observed; 51, the same individual after several days in a moist chamber.

Rôle. — Most moss rhizoids clearly are organs of anchorage, though the stem felts common in swamps and in moist woods are of no importance in this respect. The scantiness of experimental data makes it impossible to speak in general terms concerning the efficiency of the

rhizoids in absorption. Probably mosses like *Polytrichum*, which grow as detached individuals and possess " vascular " strands and extensive rhizoids, are able to absorb water and salts through the latter; indeed, the rise of colored liquids has been witnessed in the rhizoids of *Polytrichum*. When the rhizoids of *Catharinea* are severed in the soil, the leaves wither precisely as they do in seed plants when the roots are cut. Water drops appearing on cut stem surfaces of *Mnium* have been supposed to indicate conduction and hence rhizoid absorption. In *Polytrichum* and in *Catharinea* the rhizoids are intertwined like the strands of a rope, so that doubtless water can ascend between them by capillarity as well as within them. In mat and cushion mosses it is probable that leaf absorption, facilitated by the ready capillarity made possible by close contact between adjoining shoots, is much more important than is rhizoid absorption (p. 126).

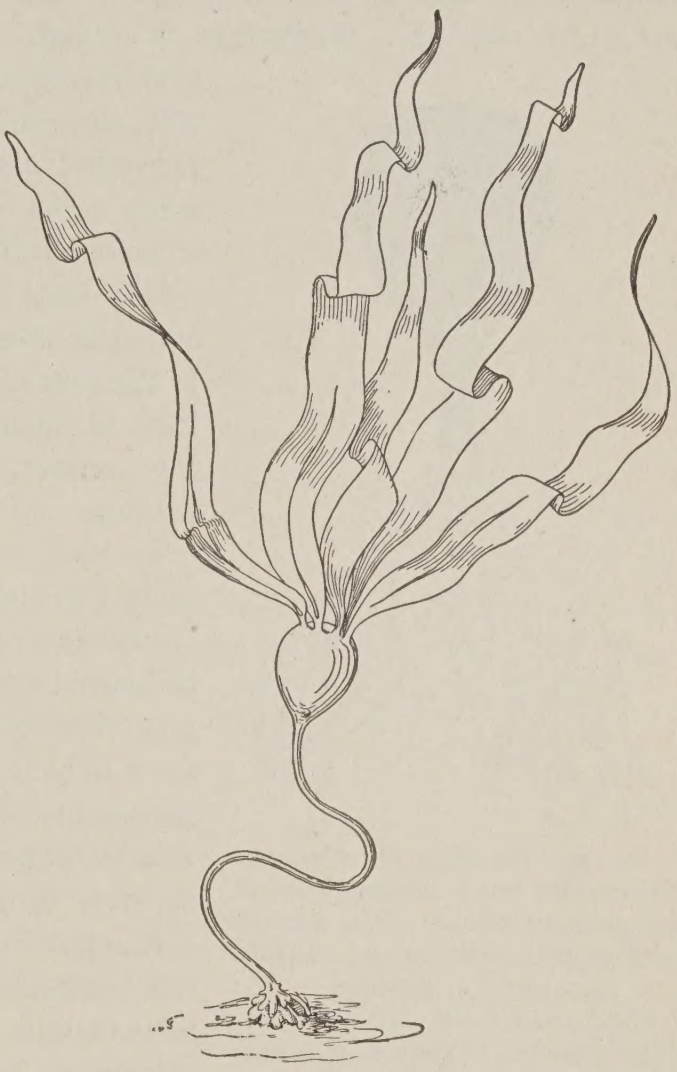


FIG. 52. — A marine alga (*Nereocystis*), showing a rhizoid complex or system of haptera, which serves as a holdfast organ, fixing the plant firmly to a rocky substratum below sea level; note the stalk or stipe, whose bladderlike expansion floats the leaflike organs at the water surface. — From COULTER (Vol. One).

Rhizoids of algae and of lichens. — *Algae.* — Many small algae are entirely unattached, and move actively (*Volvox*) or drift passively (*Pleurococcus*). Other forms are attached by the mucilage they exude. Some filamentous algae (as *Ulothrix* and *Oedogonium*) are anchored by

the basal cell, which may differ from the other cells in shape and color; such forms often are epiphytic on other water plants. Rootlike rhizoids occur in *Vaucheria*, *Botrydium*, and *Chara*. Large marine algae are attached to rocks by much-branched rhizoids (or *haptera*) of considerable size, though they are simple and undifferentiated in structure (fig. 52). Anchorage is thought to be the chief rôle of such rhizoids, and it is an important rôle, since marine algae are especially prevalent along rocky coasts, where wave action is violent. The hairlike rhizoids of *Botrydium* (fig. 53) and of *Chara* may be of value also in absorption, as seems to have been proven in the case of *Chara*. Rhizoid formation in algae is determined largely by contact, especially with rough surfaces.

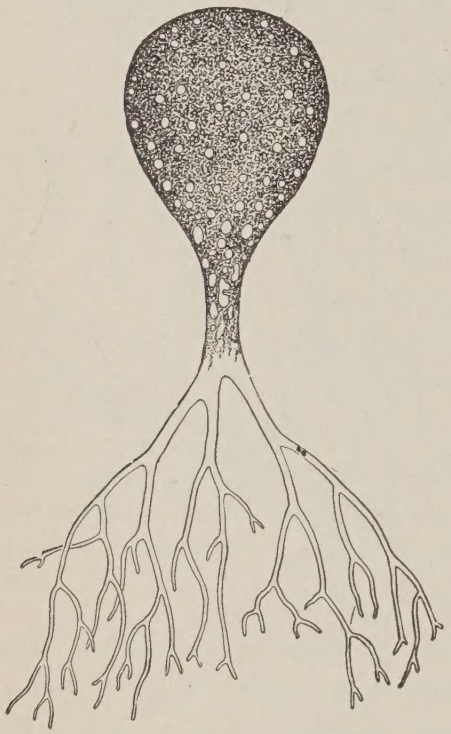


FIG. 53. — A plant of *Botrydium*, showing the much-branched colorless subterranean rhizoid system and the globular green aerial portion; the plant is a coenocyte, *i.e.* multinucleate but without internal cell walls; considerably magnified. — From ROSTAFINSKI and WORONIN.

Lichens. — Lichens usually are attached to the substratum by rhizoids (or *rhizines*) which may have hairlike or discoid tips. These rhizoids are of great importance as holdfast organs, since lichens usually grow in exposed situations, where they might otherwise be blown away. Lichens are able to grow directly on bare rocks, and this is partly because the rhizoids exude substances which corrode the substratum; especially is this true of calcareous lichens, some of which become almost entirely embedded within the rock. Possibly lichens are able also to absorb water and solutes through their rhizoids.

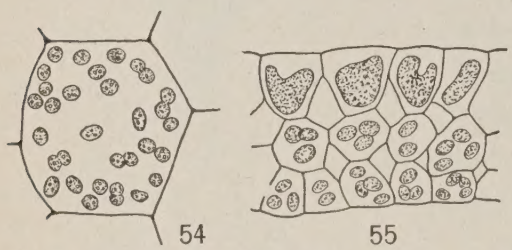
Concluding remarks on roots and rhizoids. — Often the progress of evolution has been along the line of a division of labor. Such seems to have been the case in the evolution of organs of absorption and of anchorage. Among the algae the entire plant body takes part in the absorption of water, salts, and gases, though primitive anchorage organs are represented by the haptera. In the bryophytes, rhizoids

are generally developed, and probably they are organs of absorption as well as of anchorage, though the plant body still takes an important part in absorption. In the ferns and seed plants, the roots are the chief anchorage organs, and the young roots with their hairs are the chief organs of water absorption, while the leaves are largely without absorptive efficiency.

CHAPTER II — LEAVES

1. CHLOROPHYLL AND FOOD MANUFACTURE

Introductory statement. — Leaves usually possess a more or less expanded portion, the *blade*, which may or may not be borne on a stalk, the *petiole*. The blade is composed of *veins* and of the green parts between the veins, the *mesophyll;* the latter is the seat of food manufacture, and the former are organs of support and transportation. In many cases leaves are scalelike and take no part in food making, while, on the other hand, stems frequently have an important part in this process. The chief foods manufactured by plants are *carbohydrates* (such as the various sugars and starches), *fats*, and *proteins* (such as the albumins). The simplest of these foods, the carbohydrates, are manufactured first, and most of our knowledge of food making deals with this synthesis of carbohydrates.



FIGS. 54, 55. — Chloroplasts: 54, a cell from a moss leaf, showing chloroplasts in various stages of division; the bodies within the chloroplasts are starch grains; 55, a cross section of a leaf of *Selaginella martensii*, showing two kinds of chloroplasts, those in the lower part of the leaf being small and resembling the chloroplasts of 54, while those in the upper epidermis are large and solitary; note the irregular shape of the latter, some being more or less mortar-shaped, the maximum surface exposure being toward the light; note also the thinness of the leaf (three cells thick); both figures highly magnified.

Chloroplasts and chlorophyll. — *The chloroplasts.* — The synthesis of carbohydrates, or *photosynthesis*, is associated with the green bodies of plant cells, the *chloroplasts*, which consist of a colorless, protoplasmic, spongelike matrix, the *stroma*, impregnated in the peripheral portions, with a green pigment, the *chlorophyll.* In shape, chloroplasts generally are somewhat spheroidal or ellipsoidal (or even polygonal, if crowded), the number in a cell varying from few to many (fig. 54; also fig. 59). However, in the Conjugales and in many other algae there are one to

several large chloroplasts in a cell, which may be tabular, spiral, cylindrical, cuplike, or stellate in shape. In *Anthoceros* and *Selaginella* the chloroplasts in some cells are many and small, while in other cells they are few and large (fig. 55). Sun plants commonly have smaller chloroplasts than do shade and water plants. The so-called *chromoplasts* of carrot roots, nasturtium flowers, etc., often are irregular in shape (fig. 56).

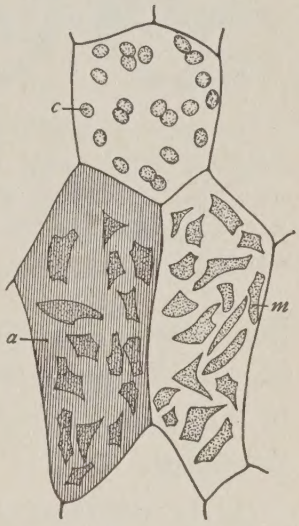


FIG. 56. — Cells from a perianth segment of the nasturtium (*Tropaeolum*), showing variations in the form of chromoplasts, some (*c*) resembling chloroplasts in shape, while others (*m*) are irregular in outline; these chromoplasts are yellow or orange in color; in addition there may be a red pigment, anthocyanin, diffused in the cell sap (position here indicated by lines, *a*); highly magnified.

The pigments. — The green color of the chloroplasts is due to a mixture of two green and two yellow pigments. The green portion, or true *chlorophyll*, consists of an olive green component known as *chlorophyll* α and a yellow green component known as *chlorophyll* β. Associated with these green pigments are smaller quantities of an orange pigment known as *carotin* and a yellow pigment known as *xanthophyll*. The amounts of these different pigments in different leaves vary somewhat but usually there is about three times as much green pigment as yellow and about three times as much chlorophyll α as chlorophyll β. These pigments are not soluble in water and are therefore never found dissolved in the cell sap. The leaves of succulent plants, salt plants, and epiphytes are usually pale green in color in contrast with the dark green of such leaves as those of the beech and pine. The different shades of green leaves may be due in part to differences in the composition of the mixed pigment and in part to the number and size of the plastids.

Miscellaneous features. — Chloroplasts contain various inclusions, notably starch grains (fig. 57; also fig. 34); the *pyrenoids* of algae and of *Anthoceros* are protein inclusions, and oil is common, especially in dying plastids. Plastids arise by division from preëxisting plastids (fig. 54), and at times *de novo* in the cell cytoplasm, from the development of minute organs of the cell known as *mitochondria*. A careful search usually reveals the presence of plastids, even where their absence might be expected (*e.g.*, in embryos). Although chlorophyll usually occurs only in chloroplasts, spectroscopic tests

show its presence in the blue-green algae and in *Cuscuta*, where ordinary chloroplasts probably are lacking.

The influence of external factors upon chlorophyll development. — *Light.* — The general necessity of light for chlorophyll development is shown by the pallor of shoots that develop in the dark (*e.g.* celery leaves and potato sprouts). However, less light is needed in some cases than in others, as appears from the chlorophyll layer beneath the bark in trees, and from the mosses that grow in relative darkness in the mouths of caves. If sugars and other foods are present in sufficient amount, conifer seedlings, various ferns and liverworts, and many algae become green, even in total darkness, and a number of angiosperm seedlings become green in the dark, if the fruits in which the seeds develop are produced in the light.

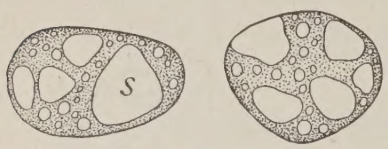


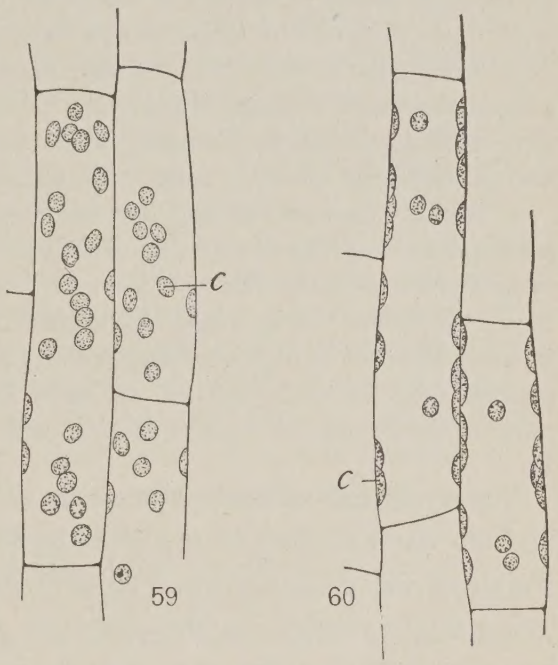
FIG. 57. — Two chloroplasts of *Rhipsalis* with several grains of starch (*s*) and many minute oil drops; highly magnified. — From SCHIMPER.

On the other hand, various algae have been observed to lose their green color when grown in rich nutrient media in the light, thus becoming physiologically equivalent to fungi. *Cuscuta* develops chlorophyll in sunlight when grown on a starved host or in water, and redwood shoots without chlorophyll have been observed to behave similarly when detached from the parent tree and placed in water. Perhaps an excess of food, though necessary for chlorophyll production in the dark, may be less necessary or even unfavorable in the light. Carotin and xanthophyll are less dependent upon light than is chlorophyll, remaining longer when plants are placed in darkness, and appearing sooner when they are placed in the light.

FIG. 58. — An albescent leaf of *Abutilon:* the shaded portions represent the parts containing chlorophyll, the other portions being colorless; note the greater development of those parts where the chlorophyll is more abundant.

Temperature and salts. — Low temperatures are more detrimental to chlorophyll than to xanthophyll, the latter appearing first in spring and remaining latest in autumn; the yellowing of evergreens in winter illustrates the same principle. The development of pallid shoots at low temperatures has been observed in *Sequoia* and in *Brassica*. Iron salts and nitrates are regarded as favorable for chlorophyll development, whitening due to lack of iron being called *chlorosis;* common salt impedes chlorophyll development, and perhaps is responsible for the pale color of salt marsh plants, as has been shown to be the case in *Salicornia*. Plants attacked by parasites often show chlorophyll impairment.

Albescence. — In many plants, especially in certain variegated plants cultivated for ornament (as *Abutilon* and *Caladium*), the absence of cholorophyll is not obviously related to external factors. Yellow spots contain plastids colored with xanthophyll, and white spots lack even plastids. Such plants are propagated readily by cuttings and sometimes also by seed. It is evident that there are in *Abutilon* and other variegated plants at least two sorts of albescence; a common kind that is hereditary and not infectious, and a rare kind that is infectious and not hereditary. Whitening or *albescence* of the latter type in *Abutilon* is thought to be due to a virus (perhaps an enzyme) that is detrimental to chlorophyll development; in any event, green plants may become variegated by grafting. The boundaries of the white spots usually are veins, which perhaps act as barriers to the virus. White spots exposed for a time to darkness and then to light become green, as though the virus were destroyed by darkness. In some plants (fig. 58), but not in all, the albescent leaves or parts of leaves are smaller than those that are green, indicating defective food migration from other parts.



FIGS. 59, 60. — Variations in the form and position of chloroplasts (*c*) in *Isoetes:* 59, a surface view of epidermal cells that have been exposed to diffuse light; the position taken is that of epistrophe; 60, similar cells that have been exposed to direct and rather intense sunlight, illustrating apostrophe; note that the chloroplasts near the walls differ in shape from those found elsewhere; highly magnified.

The movements of chloroplasts. — In diffuse light, plastids commonly are close to the outer cell walls, and so arranged as to expose a maximum surface to the light (*epistrophe*, fig. 59). When exposed for a time to intense light, the plastids for the most part move to the side or rear walls, to which they are closely appressed, and their chief axis is parallel rather than perpendicular to the incident light (*apostrophe*, fig. 60). If exposed to intense or long-continued light, the plastids tend to become grouped in the center of the cell (*systrophe*). These movements commonly are believed to be advantageous. The advantage of epistrophe is obvious, since light is so important for the development and rôle of chlorophyll. The advantage of apostrophe is less obvious, though there are reasons for believing that chlorophyll is injured or destroyed in intense light. The alga *Mougeotia* has plate-

like plastids which stand on edge in intense light and have a horizontal position in diffuse light.

The usual view has been that plastids are not actively motile but drift passively in cytoplasmic currents, though there is some evidence that they exhibit amoeboid movements, reacting chemotactically to carbon dioxide and to other substances unequally distributed in the cell; in any case it is clear that they change their form as conditions change (figs. 59, 60). Other factors than light cause change of position, notably changes in temperature and in water content. In *Dictyota*, apostrophe is caused by immersion in water of higher concentration than sea water, while immersion in water of lower concentration results in epistrophe. Possibly the plastid movements commonly referred to changes in light intensity may be due in part, at least, to osmotic changes; at all events, the effects of reduced water supply and of high light intensity seem to be the same.

It is likely that plastid motility has been too much emphasized. Intermediate positions are much more common than either apostrophe or epistrophe. Sun plants in particular have plastids that are relatively immotile, the position of apostrophe (profile position) being usual in darkness as well as in daylight (fig. 67). The greatest motility is found in water plants and in shade plants; in sun plants the plastids near the under surface are more likely to change their position than are those in the elongated or palisade cells near the upper surface.

The synthesis of carbohydrates. — The water absorbed by the roots and the carbon dioxide absorbed by the leaves combine in the latter in the presence of sunlight and form elementary *carbohydrates*, the process being accompanied by the emission of oxygen. Generally the theory has obtained that the first carbohydrate formed is formaldehyde, and that later through its condensation there develop sugars, which may migrate as such through the plant or which may be transformed into starch by the plastids; in the blue-green algae, glycogen is an early synthetic product, and fatty oils are the first visible products in *Vaucheria* and in diatoms. The discovery of formaldehyde in the plastids of numerous leaves tends to confirm this theory, the objection that it is poisonous to plants being met by assuming that it at once becomes condensed into harmless carbohydrates.

The influence of external factors upon carbohydrate synthesis. — *Light.* — Whatever may be its specific rôle, light is fundamentally important in the early stages of food-making. There is a minimum intensity of light below which synthesis is impossible, and a certain intensity above which the amount of manufactured food decreases, each plant having its optimum light relation. This optimum usually is much lower for shade plants and water plants than for sun plants, but in all cases a decrease of light below the optimum im-

pairs synthesis much more than does an increase of light above the optimum.

It is not clear why increased light should ever cause reduced food production; possibly it is because the enzymes or the chlorophyll itself are ill-adapted to withstand intense light, and it may be that the maximum activity of the chloroplasts is impaired by their assumption of the profile position. In bright sunlight only a fraction of the light available for synthesis is thus utilized. The depth at which green plants are found in the sea is slight, doubtless because at a depth greater than twenty meters the light generally is insufficient to initiate food-making. While green algae (*e.g. Halosphaera*) have been brought up from great ocean depths, it is likely that they have sunk from their place of development near the surface. Red algae grow at greater depths than do most chlorophyll-bearing plants, and it has been thought that their color makes this possible (see p. 45). Probably sulphur bacteria and nitrifying bacteria are able to manufacture carbohydrates at great depths because of their independence of light. The chlorophyll layer beneath the bark of trees is known to manufacture carbohydrates, although the light intensity must be low.

The absorption spectrum of chlorophyll shows that rays toward the red and the blue ends of the spectrum are absorbed more completely than are the intermediate rays, and usually it has been supposed that the red, orange, and yellow rays are more efficient in carbohydrate synthesis than are the blue rays, the green rays being the least efficient of all.[1] It has been held that the color of chlorophyll is of adaptive significance, since it absorbs the more useful red rays rather than the less useful green. This theory lacks adequate support; the absorption spectrum of blood is quite as remarkable as is that of chlorophyll, but the color has no adaptive significance. The color of blue-green algae may be of significance, for it appears that in many forms (*e.g.* in *Oscillatoria*) developing cells assume a color complementary to that of the incident light; the red alga, *Porphyra*, is said to become green if grown in red or yellow light. It is not known whether these chromatic changes have any effect upon the synthesis of carbohydrates; some investigators doubt the existence of such changes.

Temperature; carbon dioxide; water. — In the laurel cherry, synthesis takes place only between $-6°$ C. and $45°$ C., while the limits of effective synthesis are still narrower. The limits and the optima vary with the species, being lowest in arctic and alpine forms, where effective synthesis can take place below $0°$ C., though probably not so far below as sometimes has been thought. The optimum temperatures usually are rather high (from $20°$ C. to $22°$ C. in many plants). The rate of carbohydrate synthesis varies also with the carbon dioxide available, the amount commonly present being too low for optimum synthesis. There is ground for believing that an optimum amount of carbon dioxide has been present in certain geological ages, which might account

[1] It seems probable that light rays are utilized in proportion to their wave length, the longer being more efficient than the shorter, if of equal energy value.

for the extreme luxuriance of the vegetation then existing. In dry soil the water supply may be insufficient for optimum synthesis. It is probable that temperature, carbon dioxide, and water, more often than light, are limiting factors. In the Mediterranean region, winter synthesis is slight because of low temperature, while in summer it is slight because of desiccation; since the stomata close in dry weather, desiccation is likely to result in a decrease of carbon dioxide as well as in a decrease of water.

Starch formation. — The synthetic process above outlined culminates in the formation of sugars, which readily pass as solutes from cell to cell. During the day sugar is manufactured more rapidly than it can be transported, and the excess, for the most part, is converted into *starch*, which accumulates in the chloroplasts. During the night this starch is reconverted into sugar and removed from the working cells. Thus the accumulation of starch in the chloroplasts is a measure, not, as has been thought, of the working capacity of a leaf, but of the excess of sugar-making over sugar transportation. Starch-making is a function of the plastids, not only of the chloroplasts but also of colorless plastids (*leucoplasts*); it takes place in the dark (*e.g.* in potato tubers) as well as in the light. Starch manufacture is favored by high rather than by low temperatures; hence, as might be expected, sugar generally replaces starch in winter leaves.

The synthesis of proteins. — Comparatively little is known concerning *protein-synthesis*, which seems to be a process common to all plants. The chief necessity is a supply of carbohydrates and of available nitrogen. In green plants the chlorophyll-bearing cells probably are the chief seat of protein-synthesis as of carbohydrate synthesis, and the process seems to take place chiefly in the light, though neither light nor chlorophyll is necessary if the carbohydrate supply is adequate.

Anthocyanins. — *General features.* — Contrasting with chlorophyll, xanthophyll, and carotin, which occur in plastids, are the red pigments (*anthocyanins*) of many leaves, which usually are dissolved in the cell sap (occasionally occurring as crystals or grains), and thus are disseminated uniformly throughout the cells where they occur. They are most familiar, perhaps, in dying autumn leaves, but are common in young leaves (especially in spring), and occur at times in winter leaves and in shade leaves (especially beneath), while in some plants (as *Coleus*) they are always present. The pigments may be in the epidermis (as usually in floral leaves and in developing foliage leaves), or they may occur in the chlorophyll-bearing cells (as usually in dying foliage leaves), or in both, and the leaf may appear uniformly colored, or colored chiefly on the veins or over the mesophyll (fig. 56). The same pigments occur in flowers, where other colors than red, especially blue, are frequent. In alpine regions anthocyanins are more abundantly developed both in leaves and in flowers than they are in the lowlands.

The factors concerned in anthocyanin production. — Anthocyanins commonly are accompanied by an excess of sugar, and premature coloration may be induced in the leaves of plants by growing them in concentrated cane-sugar solutions. Low temperatures often have been assigned as a cause of red coloration, and, since sugar tends to accumulate at low temperatures (starch formation being relatively unusual), the sugar and temperature theories of pigmentation seem to harmonize. It is probable also that the development of the absciss layer (p. 98) tends to impede sugar migration from the leaf to the stem, thus facilitating anthocyanin production. Decortication and probably all other factors that retard conduction facilitate the formation of anthocyanin; furthermore, drought may incite brilliant coloration even in midsummer. The cause of spring coloration is less obvious, but it may be associated with the flow of sugar into the developing leaves. Usually those species that color most in autumn also color most in spring, and among the more highly colored plants are many in which tannins are produced in abundance, as oaks and sumacs. A current view of the composition of the anthocyanins is that they are oxidized glucosids. Sunlight usually facilitates anthocyanin production, perhaps accounting for the general predominance of color on the upper leaf surface, and for the occasional high color on the morphologically under surface of upturned wilted leaves; sunlight also may account for the high coloration in open situations as compared with that in dense woods. Certain roots, as those of the corn and the willow, color in the sunlight. Many flowers and fruits color in complete darkness, if there is an adequate food supply.

The rôle of anthocyanin. — Whether leaf anthocyanin is of any advantage to plants is very doubtful. Some investigators have regarded the red pigment as a screen that absorbs those rays which are injurious to chlorophyll or which tend to inhibit the migration of carbohydrates. Another aspect of the screen theory is that anthocyanin absorbs the violet and ultraviolet rays, which are injurious to the leaf enzymes. There is slight experimental evidence for any aspect of the screen theory. A commoner view is that anthocyanin absorbs certain rays which increase the leaf temperature and hence increase the efficiency of the chlorophyll. Red-leaved varieties of certain species (*e.g.* the copper beech) seem to have a slightly higher leaf temperature than do green-leaved varieties, as is indicated by the temperature of solutions in which the leaves are placed, by the rapid melting of cocoa butter, and by thermoelectric measurements. These temperature differences, however, are so slight as to seem inconsequential, the maximum difference observed being four degrees.[1] The red color of deep-water algae has been thought to be advantageous, because of its power to absorb the blue rays, which penetrate deeper than do the others; red rays penetrate scarcely below fourteen meters, a depth at which red algae are the dominant forms. Few of the theories here mentioned are more than guesses, and it may be that the red pigments are merely the indices of certain chemical activities that are quite without functional significance. Various annuals (*e.g. Chenopodium*) assume vivid colors just as they are dying, and any advantage in such coloration is most improbable. It is not unreasonable to suppose that plants may have many useless organs and characters, which are mere by-products of their fundamental activities.

[1] Red leaves, as a rule, contain less chlorophyll than do green leaves, so that on the whole the former probably are the less efficient working organs.

2. THE STRUCTURE AND ARRANGEMENT OF CHLORENCHYMA

Structural variations in chlorophyll-bearing tissues. — *Mesophytic dicotyls.* — The tissues that contain chlorophyll, *i.e.* the *chlorenchyma*, show considerable diversity, referable in large part to environment. Most mesophytic leaves lack epidermal chlorophyll (except in the guard cells of the stomata), but most of the internal cells except those in the conductive tract contain chlorophyll, more being present in the upper than in the lower half. The cells of the upper portion, known as *palisade cells* (or, simply, as *palisades*), are elongated transversely to the leaf surface (especially in dicotyls), and are arranged in one to three compact layers (figs. 61, 62). The cells of the under portion, the *spongy parenchyma* (or, simply, the *sponge*), are arranged loosely and irregularly and have prominent intervening air spaces, the *lacunae*. Both the palisade cells and the sponge cells have thin, permeable, cellulose walls.

Mesophytic monocotyls; hydrophytes and shade plants. — The leaves of many mesophytic monocotyls, especially among the grasses and the sedges, have a somewhat compact and uniform chlorenchyma without palisade cells (fig. 63), and some monocotyls have cells elongated parallel to the leaf surface. In submersed hydrophytes epidermal chlorophyll usually is abundant (fig. 325), often exceeding in amount

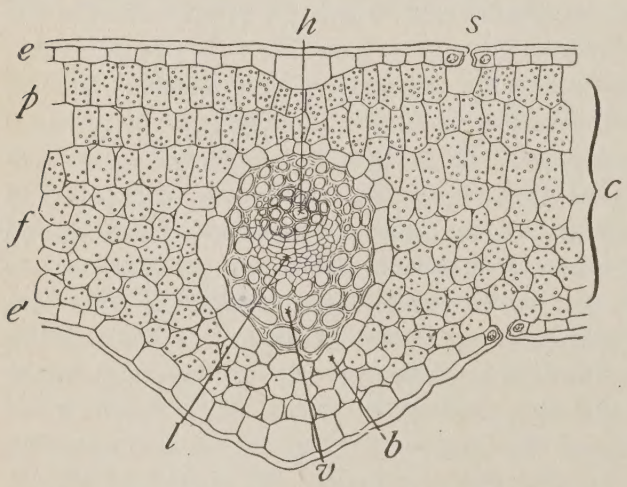


FIG. 61. — A cross section of a mesophytic leaf, that of a peppergrass (*Lepidium*), showing the upper epidermis (*e*), the lower epidermis (*e'*), stomata (*s*), the chlorenchyma (*c*) consisting of closely placed palisade cells (*p*) and more loosely placed sponge tissue (*f*), and a vascular or conductive tract (*v*) with bundle sheath (*b*), hadrome or xylem (*h*), and leptome or phloem (*l*); considerably magnified.

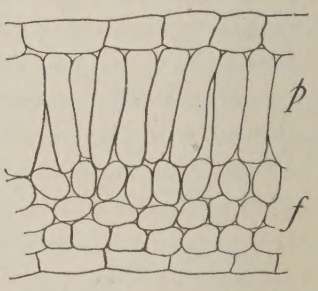


FIG. 62. — A cross section of a mesophytic leaf, that of a blue violet (*Viola cucullata*), showing a single row of greatly elongated palisade cells (*p*), beneath which is a region of loose spongy tissue (*f*); considerably magnified.

that contained in the mesophyll, which may be loose and spongy by reason of the large air spaces, or which may be reduced to a single layer (fig. 64). Hydrophytes with emersed leaves are much like mesophytes, except for

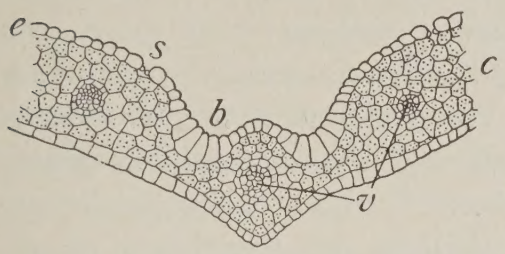


FIG. 63. — A cross section of a mesophytic grass leaf, that of the blue grass (*Poa pratensis*), showing relatively uniform chlorenchyma (*c*), an upper epidermis (*e*) differing considerably from the lower, especially in the large cells (*b*) which are concerned in leaf movement; note the vascular tracts (*v*) and observe that the stomata (*s*) are confined to the upper surface; considerably magnified.

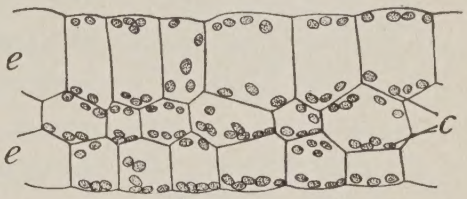


FIG. 64. — A cross section of a submersed hydrophytic leaf, that of a pondweed (*Potamogeton lucens*), showing the few cell layers (here three) characteristic of a water leaf; note the abundance of chloroplasts (*c*) in the epidermis (*e*) and the absence of cutinized epidermal walls; highly magnified.

their large lacunae (fig. 109). Shade plants are weak in palisade tissue, but, except in ferns (fig. 55), they rarely contain epidermal chlorophyll. In some leaves, especially in shade plants (such as *Maranta* and *Asarum*), the convex outer walls of the epidermal cells converge the rays of incident light; the reflection of some of these rays gives a velvety aspect to the leaf (fig. 65). Occasionally (as in *Fittonia*) isolated epidermal cells, known as *ocellae*, are more papillate than are their neighbors. It has been supposed on somewhat uncertain evidence that epidermal cells with convex outer walls are organs of light perception. A more probable rôle of such cells is the facilitation of synthesis through light convergence. In the luminous moss, *Schistostega*, the chloroplasts are near the base of a globose cell, which, acting as a lens, converges the light upon the plastids; the emission of reflected rays causes this moss and the alga, *Botrydium*, to glisten in the sunlight. The leaves of water plants and of shade plants are deep green, which is due partly to the thin, transparent epidermis and partly to the peripheral position of the numerous deep-green chloroplasts.

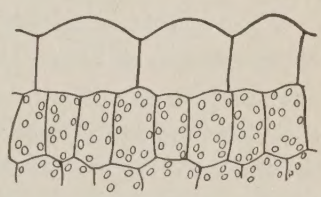


FIG. 65. — A cross section of the upper part of a shade leaf, that of the wild ginger (*Asarum canadense*), showing three epidermal cells with convex outer walls which converge the rays of incident light; considerably magnified.

Xerophytes. — Xerophytes contrast sharply with hydrophytes, displaying prominent palisade tissue, often in many rows (as in the oleander and in most cacti), while the spongy tissue is small in amount and poor in air spaces, and often is best developed toward the leaf center (fig. 113). Frequently there are palisades in the lower half of the leaf, though less prominently developed than above; in the cottonwood the palisades are developed nearly equally on the two sides, and in many fleshy vertical leaves there is a cylinder of palisade cells about the colorless leaf interior (figs. 232, 233). Xerophytic leaves commonly are thick, and succulent xerophytic leaves often are without chlorophyll at the center; sometimes also the epidermis is several cells thick and free from chlorophyll (figs. 67, 234). Some succulent xerophytes, notably the Crassulaceae (fig. 231) and many xerophytic grasses (fig. 141), are quite without palisade tissue, but the compactness of the chlorenchyma distinguishes them from hydrophytes. Xerophytic leaves usually are pale green in color, by reason of a relatively non-transparent epidermis (due to hairs, wax, or cutin) or by reason of the deep position of the chlorenchyma; or the chloroplasts may be pale in color or relatively scattered in position. Thick leaves with compact tissues and prominent palisade layers characterize not only the plants of ordinary xerophytic situations, but also those of peat bogs and salt marshes. Alpine plants have more palisade tissue than do arctic plants, while the latter have a more lacunar sponge tissue.

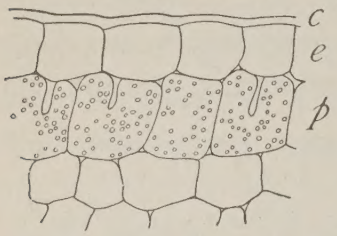


FIG. 66. — A cross section of the upper part of a lily leaf (*Lilium longiflorum*), showing the so-called arm palisades (*p*), also the upper epidermis (*e*) with its cuticle (*c*); considerably magnified.

Taxonomic variations. — In some leaves, as in *Sambucus* and *Lilium* (fig. 66), there are *arm palisades*, in which wall infoldings give an increased inner surface to the cell; in pine leaves wall infoldings are remarkably developed, and the outer cells are divided into palisade-like compartments (fig. 346). In some succulents, as in *Portulaca* and *Begonia* (fig. 67), there are funnel-shaped palisade cells with large and immotile chloroplasts crowded at the narrow base near the conductive tract; sometimes there is a festoon of such cells about the conductive bundle (fig. 68), and occasionally palisade cells curve toward the bundle.

In most of the lower plants the chlorophyll-bearing cells make up the body of the plant and are not delimited into special tissues. In the red algae there are elongated cells arranged somewhat as are palisade cells. Most moss and liverwort leaves consist of a single layer of green cells, but in *Sphagnum* colorless cells alternate with the green cells (fig. 205); the leaves of *Leucobryum* are three cells thick, the chlorophyll-bearing cells being centrally placed (fig. 206). In the air

chambers of some thalloid liverworts (as *Marchantia*, fig. 102) there are loose cell filaments, which contrast with the compact tissues elsewhere; in the leaf of *Polytrichum* similar filaments form vertical plates hanging loosely from the leaf body. Near the base of some moss capsules the chlorenchyma is differentiated into palisade and sponge tissue, much as in seed plants. In lichens the chlorenchyma consists of the algal layer, which lies close to the surface in shade forms and deeper in sun forms (fig. 418).

The influence of external factors upon the form and orientation of chlorenchyma cells. — *The plasticity of chlorenchyma.* — Chlorenchyma is one of the most plastic of plant tissues, its thickness, its compactness, and even its differentiation into palisade and sponge often being subject to environmental control. However, there are many cases of rigidity, as in most monocotyls and in some dicotyls (*e.g.* in the Crassulaceae), where no condition seems to induce palisade development; in various dicotyls palisades appear to develop without regard to external factors. In many cases palisades appear in the bud, where the usual palisade-producing factors can have no influence. But even in these cases there often is variation

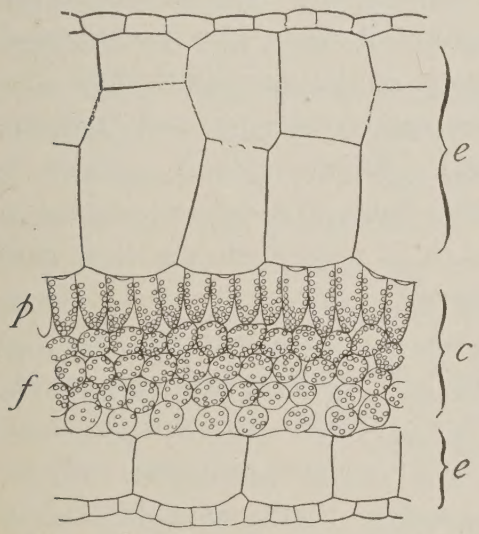


FIG. 67. — A cross section of a succulent leaf, that of *Begonia*, showing centrally placed chlorenchyma (*c*), consisting of funnel-shaped palisade cells (*p*) whose chloroplasts are grouped chiefly at the basal end, and loosely arranged sponge cells (*f*); note the heavy epidermis (*e*), averaging three cells in thickness above and two beneath, and quite without chloroplasts; such an epidermis represents a peripheral water tissue; considerably magnified.

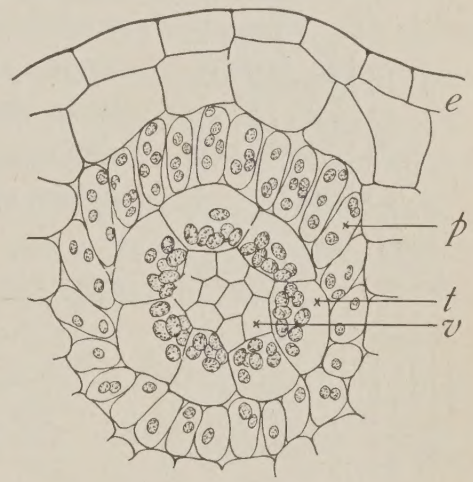
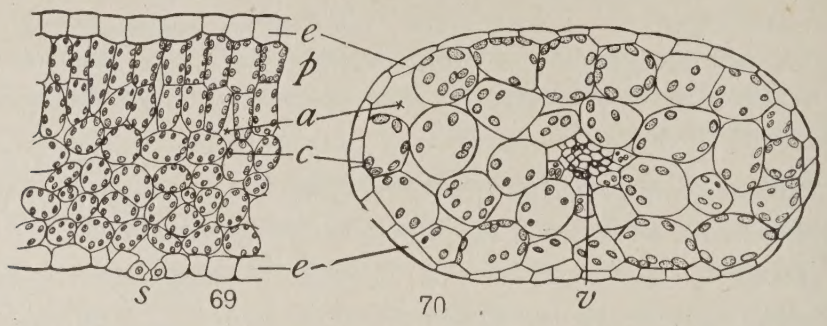


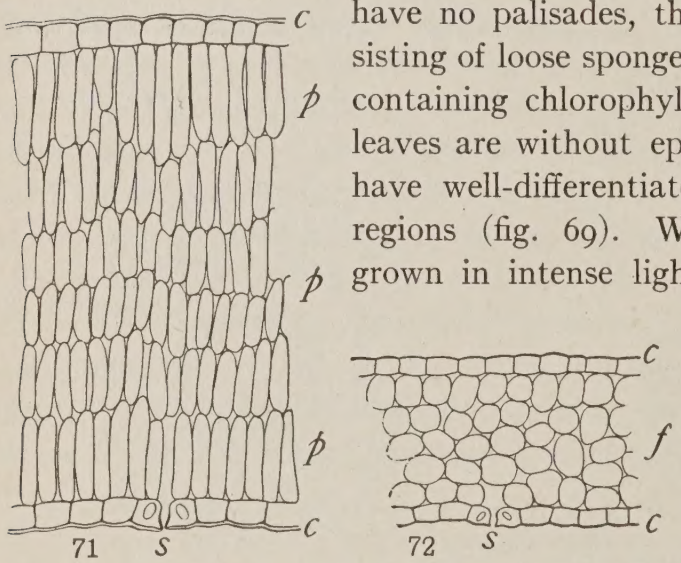
FIG. 68. — A cross section of the upper part of a succulent xerophytic leaf, that of the purslane (*Portulaca oleracea*), showing a festoon (*t*) of funnel-shaped cells with large basal chloroplasts grouped about a small vein (*v*), and an outer ring of palisade cells (*p*), containing chloroplasts of ordinary size; note that the palisades are not symmetrically placed but appear to be oriented with respect to the incident light; the epidermis (*e*) is two cells thick and represents a peripheral water tissue; highly magnified.

in cell length, in the number of palisade layers, or in compactness of tissue, showing that the environment has some modifying influence.



FIGS. 69, 70. — Leaf cross sections of the mermaid-weed (*Proserpinaca palustris*): 69, a section through a mesophytic air leaf, showing prominent palisades (*p*) and epidermis (*e*), and a stoma (*s*); 70, a section of a segment of a water leaf, showing undifferentiated chlorenchyma (*c*) made up of sponge cells, between which are prominent air spaces (*a*); the epidermis and the conductive tract (*v*, not shown in 69) are much reduced in the water form; figures equally magnified.

Among the most plastic forms are the amphibious plants, such as *Proserpinaca* and various buttercups, in which the submersed leaves have no palisades, the entire mesophyll consisting of loose sponge, and the epidermis often containing chlorophyll (fig. 70); the emersed leaves are without epidermal chlorophyll and have well-differentiated sponge and palisade regions (fig. 69). When *Lactuca scariola* is grown in intense light, the leaves assume a vertical position and have palisade layers on both sides (fig. 71); in diffuse light the leaves are horizontal and have palisades only on the upper side, and in dense shade there are no palisades at all (fig. 72). Equally extreme variation is seen in *Eucalyptus globulus*, in which the form of the leaf, as well as its position, changes from shade to sunlight, the



FIGS. 71, 72. — Cross sections of leaves of the prickly lettuce (*Lactuca scariola*): 71, a section through a leaf grown in the sunlight and thus exposed to strong transpiration; both surfaces have been exposed directly to the sun, and the chlorenchyma is composed entirely of palisade cells, though those at the center of the leaf (*p'*) are shorter than are those near the periphery (*p*); the cuticle (*c*) also is prominent; 72, a section through a leaf grown in deep shade and thus not exposed to strong transpiration; the chlorenchyma is composed entirely of sponge tissue (*f*), and the cuticle (*c*) is but slightly developed; the shade leaf also is much thinner than is the sun leaf; *s*, stoma; figures equally magnified.

sun form having palisade layers both above and below, while the chlorenchyma of the extreme shade form consists entirely of sponge. Few leaves show such extreme variation as is found in *Lactuca*, *Eucalyptus*, and in amphibious plants, but there are many plants in which the upper leaf portion may have either palisade or sponge, and many more in which the number of palisade layers, and the shape, size, and compactness of the cells may be modified considerably as conditions change.

Light and palisade development. — It was discovered long ago that the gemmae of *Marchantia* develop chlorenchyma on whichever side is exposed to the light, colorless tissue with rhizoids developing on the other side; also that the chlorenchyma develops equally on both sides of a *Thuja* branch if exposed equally to light, the palisades commonly developed on the upper surface being due to greater light exposure. These experiments, together with similar experiments on the beech and on *Lactuca* and *Eucalyptus*, as noted above, have given rise to the prevalent view that light determines the development of palisade cells. Furthermore, light often is regarded as the chief factor concerned in the orientation of palisade cells. Sometimes palisades are oblique in vertical organs, as in the leaves of *Typha* and of *Iris*, and in the stems of *Juncus* and of *Salicornia* (fig. 73), thus giving rise to the view that palisades tend to become elongated in the direction of the incident light. However, most vertical leaves and stems have transverse rather than *oblique palisades*, growth under diverse conditions rarely having any marked effect upon palisade orientation. In those leaves of *Isolepis* that hang vertically downward there are oblique palisades, but they point down instead of up, indicating that their direction is related to leaf structure and not to sunlight, and the same probably is true of most oblique palisades. Furthermore, ordinary palisade cells are transverse to the leaf surface, regardless of the position of the leaf in relation to light.

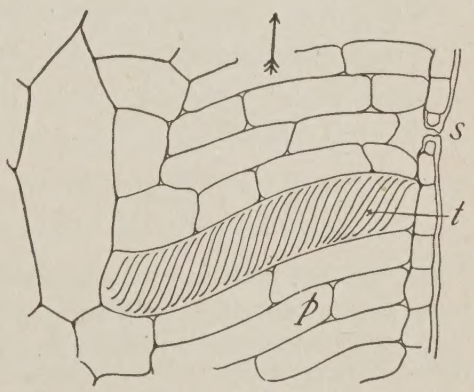


FIG. 73. — A longitudinal section through a portion of the stem of *Salicornia*, showing oblique palisades (*p*), and also a "storage" tracheid (*t*); the arrow is directed toward the stem apex; *s*, stoma; considerably magnified.

The position of the palisade layers seems relatively fixed in most cases (not in *Lactuca* and in *Eucalyptus*), a rudimentary palisade region often being discernible in the bud; in subsequent development the thickness of the layer, but not its position, may vary as external conditions vary. Thus light appears to affect chiefly the cell length, the region of development and the orientation of the palisade cells being due to other and mostly unknown causes. The influence of light upon cell elongation might be conceived of as direct or indirect. In many but not in all albescent leaves the palisades stop sharply at the edge of the green tissue (fig. 74), although the green and colorless spots are exposed equally to the light; thus palisade development appears to be correlated with the formation or with the activity of chlorophyll rather than with light directly. Again, the palisade length increases and decreases with the amount of carbon dioxide, seeming to indicate that palisade size is associated with synthetic activity.

Palisades and transpiration. — Not all cases of palisade development can be referred to light, even indirectly. For example, palisades are much better developed in dry than in wet soil, exposure to light being equal. Again, in amphibious plants there usually is an abrupt change from air leaves with strong palisades to water leaves with no palisades, although the change in light is gradual. Furthermore, it has been shown experimentally that palisades develop somewhat better in dry air with weak light than in moist air with intense light. Apparently palisade development increases with the transpiration, or,

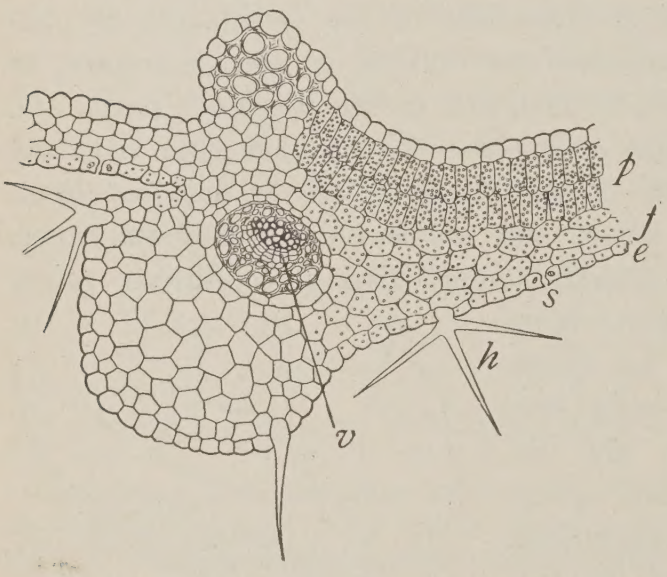
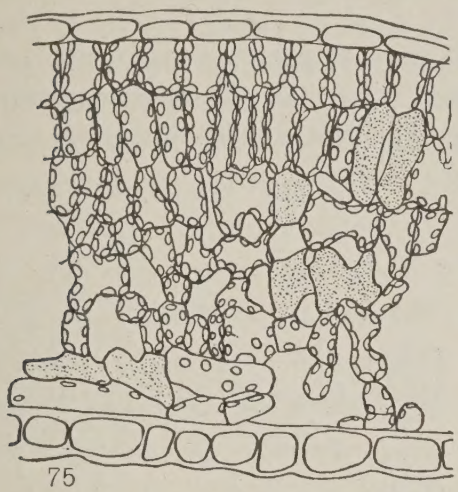
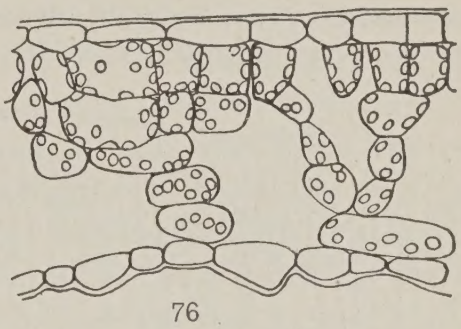


FIG. 74. — A cross section of an albescent leaf of *Abutilon;* to the right of the vein (*v*) is a chlorophyll-bearing region with two rows of palisade cells (*p*) and about three layers of sponge tissue (*f*); to the left is a colorless portion entirely without palisade cells, this part of the leaf having remained in its original undifferentiated state; the lower epidermis (*e*) contains chlorophyll, even in the albescent region of the leaf; note the lack of symmetry, due to differential growth; *h*, branched epidermal hair; *s*, stoma; *v*, vascular tract; considerably magnified.

more precisely, when there is an increase of transpiration in proportion to absorption. Even where palisade development has been referred to



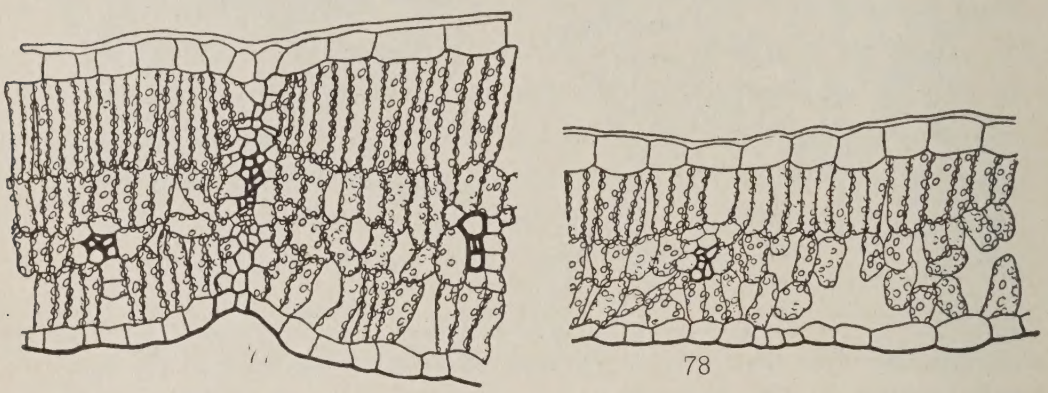


FIGS. 75, 76. — Cross sections of leaves of basswood (*Tilia americana*); (75) from the south periphery of an isolated tree; (76) from the center of the crown of the same tree; equally magnified. — After HANSON.

light, it is possible that transpiration is a factor, since increased light commonly is accompanied by increased transpiration. Thus it has been shown that the leaf blades are thicker and that there is a greater development of palisades in those leaves growing on the south periphery of the crown of a tree standing in the open as compared with leaves in the interior of the crown (figs. 75–76). The former are exposed to higher light intensity than the latter, and also are subject to higher rates of transpiration. Many bog and heath plants have thick leaves with prominent palisades. These leaves have very high rates of transpiration in proportion to the small root development of the plants. The precise action of light or of transpiration upon palisade development is not known. In the last analysis the light theory and the transpiration theory of palisade development may be essentially identical. The maximum development of palisades occurs in deserts and in other dry exposed situations where high light intensity is coupled with strong transpiration and relatively low absorption (figs. 77–78). Strong palisade development is seen also in alpine habitats, where transpiration is relatively high because of the low absorption in the cold soil. It has been shown that when leaves are arranged on upright stems those nearer the top have usually more palisade development than those inserted lower down on the stem.

Causes of variation in the position of chlorenchyma. — The most significant fact regarding variation in the position of chlorenchyma is the presence of epidermal

chlorophyll in submersed hydrophytes and in some shade plants, and its absence in other plants, except in the guard cells of stomata. No adequate cause for such variation is known, possibly because the problem has not been seriously attacked. That an external cause is probable, at least at times, is evident from the fact that various amphibious plants (as species of *Ranunculus*) exhibit epidermal chlorophyll in the water, but not in the air. Perhaps light is a factor, since epidermal chlorophyll is confined essentially to habitats where the light is of low intensity; deep-



FIGS. 77, 78. — Cross sections of leaves of the tulip tree (*Liriodendron tulipifera*); 77, from a tree on the open sand dunes; 78, from a tree in a mesophytic forest; equally magnified. — After STARR.

lying chlorophyll seems to be impossible under such conditions. On the other hand, if intense light is deleterious, the lack of epidermal chlorophyll in sun plants may be accounted for, though its absence in most shade plants would remain unexplained.

The advantages of differentiation in chlorophyll-bearing tissues. — The chief activity associated with chlorenchyma is the synthesis of carbohydrates. The palisade layers often form the chief synthetic tissue, the spongy tissue having more to do with aeration and hence with transpiration (p. 69). The palisades are relatively more efficient in diffuse light, because of their more favorable position, while in intense light the efficiency of the sponge cells increases; in very intense light they may surpass the palisades in synthetic importance, because of the deleterious effect of light upon the chlorophyll and the plastids in the latter. Experiments show that the average synthetic efficiency of palisades in proportion to sponge varies from a ratio of one hundred to thirty-six in xerophytic leaves to a ratio of one hundred to ninety-two in relatively homogeneous leaves like those of the bamboo.

Palisade cells commonly are thought to be of advantage in connection with carbohydrate synthesis, partly because light reception is favored by the absence of cross-partitions and by the parallelism of the cells to incident light, and partly because cell elongation makes possible the

motility of a relatively large number of plastids, permitting their peripheral position in diffuse light and their movement to some depth in intense light. For the most part, however, palisade orientation has been seen to be unrelated to light direction; furthermore, light commonly is present in superabundance, especially in the very plants that have the most prominent palisades, and it is in these same plants that plastid motility is slightest. Another theory concerning palisade cells is that they reduce transpiration because of their compact arrangement and the consequent reduction of their lacunae, and also because of the increased leaf thickness in proportion to the transpiring surface entailed by their presence. This theory seems quite as plausible as the one first mentioned, but the quantitative significance of the palisades in transpiration reduction is uncertain. A third theory relates palisade cells to the conductive bundles, their elongation being supposed to favor the rapid migration of the products of synthesis; there is no adequate support for this theory. A canvass of the situation fails to reveal any conspicuous advantage in palisade cells. If their shape is due to crowding, as suggested previously, no especial advantage is to be expected. In any event, no theory yet suggested has enough evidence in its favor to give it particular standing.

3. THE RELATION OF LEAVES TO LIGHT

Horizontal leaves. — Growing leaves tend to present their surfaces, especially their upper surfaces, to the incident light (fig. 79); hence, leaves are called *transversely phototropic* or *diaphototropic* organs. The simplest light relation is that in which the chlorophyll-bearing organ is more or less parallel to a horizontal substratum, as in liverworts (fig. 43), in foliose lichens (fig. 417), in rosette plants without petioles (fig. 343), in floating plants (fig. 28), and in plants with floating leaves (fig. 80). Even in such plants the shifting of the sun's position hour by hour and day by day results in great diversity of light direction; only in tropical regions are such organs strictly transverse to the dominant incident light. The fact that they are about equally horizontal at high and at low latitudes shows that some factor other than light determines their position; indeed, rosette leaves are more nearly horizontal in winter than in summer in spite of the slanting rays in the former season. However, liverworts like *Marchantia* or *Fegatella* clearly are diaphototropic, and can be induced to develop even vertical thalli if the incident light is horizontal.

FIG. 79 *A*

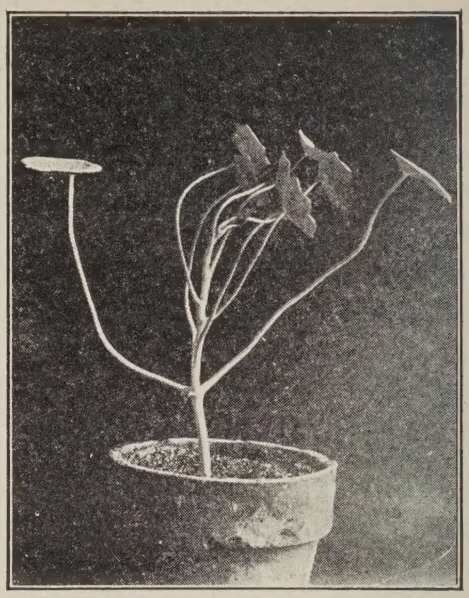


FIG. 79 *B*

FIG. 79. — Phototropism in the nasturtium (*Tropaeolum*): *A*, a plant that has been exposed since germination to ordinary greenhouse illumination; the diaphototropic leaves face upward in such a position that they receive the maximum amount of incident light; *B*, the same plant after exposure for six hours to one-sided illumination. — Photographs by FULLER.

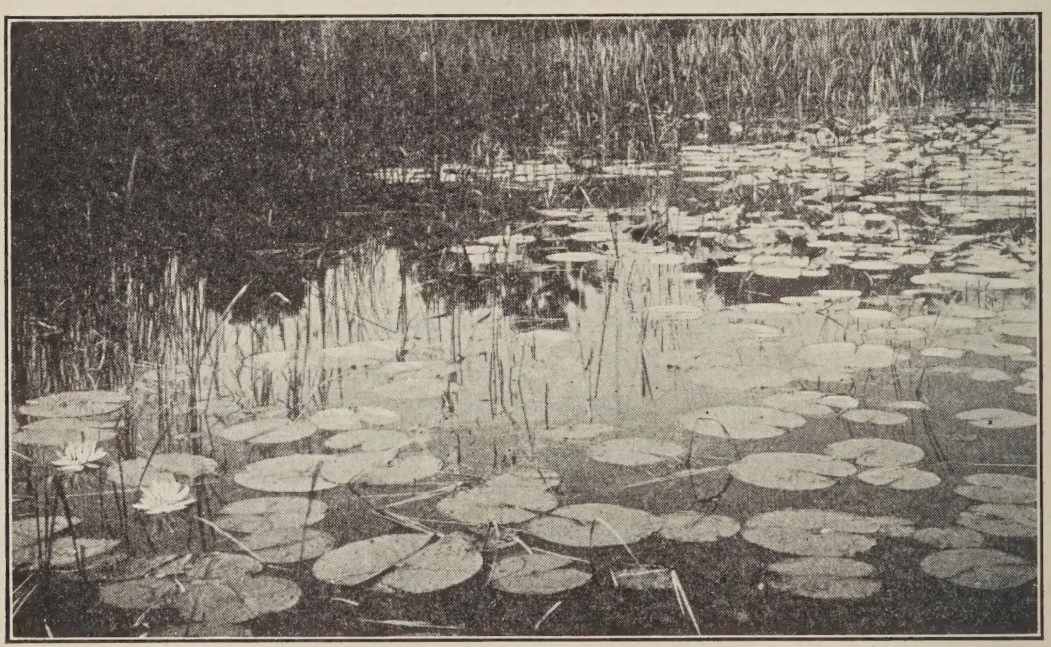


FIG. 80. — A pond margin with water lilies (*Castalia*); note that the leaves are strictly horizontal, except in the background, where they are growing so close together that their edges are upturned; shoreward from the water lilies are bulrushes (*Scirpus*) and cattails (*Typha*); Miller, Indiana. — Photograph by MEYERS.

Leaves on erect stems and their branches. — *Leaf orientation.* — Most leaves are not horizontal or even transverse to the prevailing incident light of the region where they grow. In trees and in treelike herbs and shrubs the leaves commonly face outwards and upwards on all sides (fig. 81), each leaf being transverse to those rays that are dominant for that particular leaf; leaves on the north side of a tree face north, where the sun is in the south, because more light is available from the former direction. In a plant by a window or at the edge of a forest, all of the leaves may face in one direction, because the direct light that penetrates the foliage is greater than the diffuse light on the darker side (fig. 79 *B*).

FIG. 81. — A cineraria plant (*Senecio cruentus*), illustrating a conical habit that is due to a decrease in the length and to a change in the orientation of the petioles from the base to the apex, the directional variations resulting in the assumption by each blade of a position such that it receives the maximum available light. — Photograph by FULLER.

Petioles. — During development leaves assume a position transverse to the local incident light, and this position is kept through life. The assumption of a favorable position where foliage is dense usually is due, especially in dicotyls, to the power of elongation and curvature possessed by the growing *petioles*. On vertical maple branches the petioles develop equally, but on horizontal branches every fourth leaf originates on the under side and develops a long petiole, while the opposite leaf, originating above, has a short

petiole (fig. 82). The leaf of *Tropaeolum* shows even greater plasticity, having a petiole attached to the center of the blade and capable of almost unlimited elongation and degree of curvature. In some rosette plants (fig. 343) and in plants with simple erect stems (fig. 81), the petioles are progressively shorter upward, so that the avoidance of shading is very striking. In many plants, especially

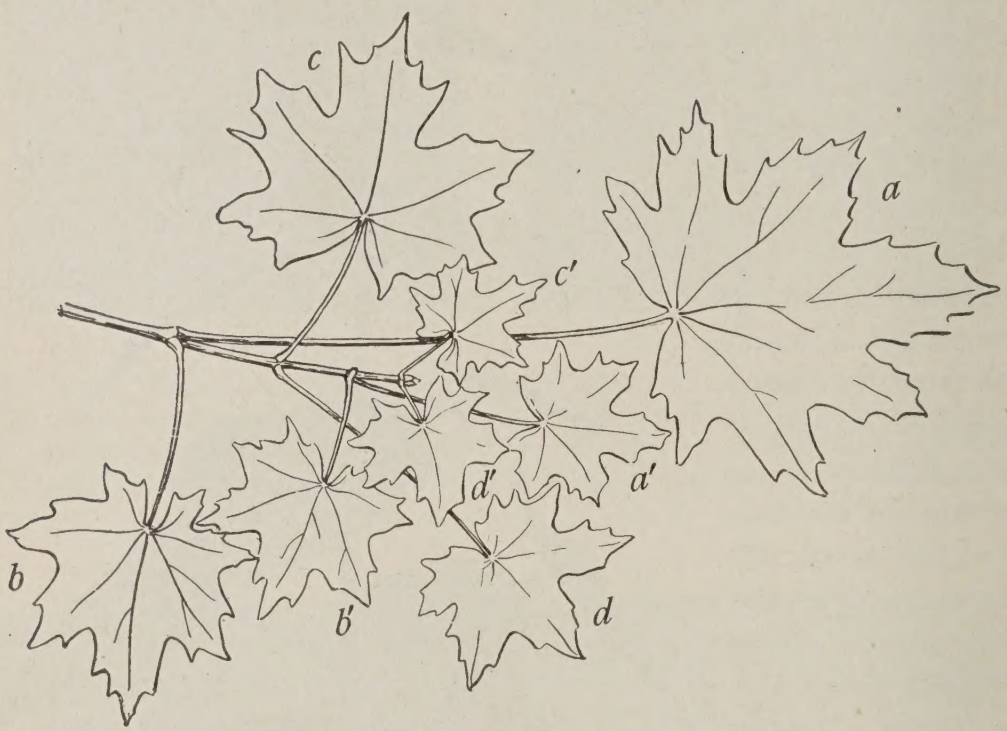


FIG. 82. — A horizontal branch of the Norway maple (*Acer platanoides*), illustrating differential petiole elongation; the palmately veined leaves are arranged in one plane facing the light, each leaf being well placed for light reception, even though the phyllotaxy is decussate; every fourth leaf (*a*, *a′*) issues from the under side of the stem and develops a long petiole, while the other member of each of these pairs (*b*, *b′*) develops on the upper side and has a short petiole; each member of the intervening pairs (*c*, *c′*, *d*, *d′*) issues from the side of the stem and has a petiole of intermediate length; note that the leaves become progressively smaller and the petioles progressively shorter toward the stem tip. — From KERNER.

in those in which petioles are wanting, stem plasticity may result similarly in advantageous leaf orientation; stem elongation is comparable to petiole elongation, and stem twisting corresponds to petiole curvature, resulting in favorable light relations for all leaves, including those that originate on the under side of horizontal stems (figs. 83, 84; see discussion of stems as organs of leaf display, p. 159).

Leaf mosaics. — Since each leaf assumes the best lighted position possible, there is in general an absence of overlapping in the leafage as

a whole, and if the foliage is dense, most of the available leaf space becomes occupied. The combined result of the absence of overlap and of the maximum occupation of space often is spoken of as a *leaf mosaic.* The perfection of this mosaic sometimes is enhanced by the fitting of projecting angles into reëntrants (as in *Hedera*), by the reciprocal arrangement of unsymmetrical leaves (as in *Celtis* and in *Begonia*, fig. 201), or by the intercalation of small leaves between larger leaves (as in *Selaginella*, fig. 202). Excellent mosaics are seen in climbing plants

FIGS. 83, 84. — Branches of a honeysuckle (*Lonicera*); 83, an erect branch, showing characteristic decussate phyllotaxy (p. 65); 84, a horizontal branch, in which stem twisting has brought the leaves into a common plane, obscuring the decussate phyllotaxy.

(as in various ivies, fig. 85), which commonly have a predominance of vertical leaves, the prevailing incident light being not far from horizontal.

Grasslike foliage. — The leaves of most grasses and sedges grow so close together that the assumption of a position transverse to incident light is mechanically impossible. In a meadow, not only the grasses, but many other plants as well, have leaves more nearly vertical than horizontal (fig. 86), and in swamps the verticality of the foliage organs among the sedges, rushes, and flags is most striking. Even such horizontal leaves as those of the water lilies have upturned edges, where the growth is dense (fig. 80). Leaf verticality or parallelism to the incident light results obviously in minimum lighting for any individual

leaf, but there is maximum lighting for the vegetation as a whole, since the more vertical the leaves, the more numerous may they be in any given space and yet have sufficient light to live. Thus the position that seems the worst for the individual leaf appears to be the best (as well as mechanically unavoidable) for the meadow or swamp vegetation as a whole, since it doubtless results in the greatest food production possible within a given volume of leafage. In many swamp plants, verticality is not due entirely to leaf crowding; in various

FIG. 85. — A "leaf mosaic" formed by leaves of the Japan ivy (*Psedera tricuspidata*), which is climbing upon a vertical wall; the leaves occupy most of the available space and yet have a minimum of overlap; though diaphototropic, they face outward and lie in a nearly vertical plane, because the dominant incident light is nearer horizontal than vertical; note the gradations between three-lobed and ternately compound leaves. — Photograph by LAND.

monocotyls (as *Typha*) the leaves are enclosed in sheaths, and in the rushes (*Juncus*, *Scirpus*, *Eleocharis*) the stems rather than the leaves often are the chief foliage organs (p. 182).

Forest undergrowth. — The relation of light to foliage is particularly evident in forests. The luxuriant undergrowth of open sunny oak woods often contrasts strikingly with the sparse undergrowth of dense shady woods of beech or hemlock, the plants in the latter consisting largely of thin-leaved mosses, ferns, and other shade plants (fig. 87). In early spring our deciduous forests are well lighted, and the undergrowth then displays remarkable activity; while in many plants the

leaves remain alive through the summer, in others they soon die (as in *Claytonia*, *Dicentra*, and *Allium tricoccum*). The great intensity of tropical light often permits a dense undergrowth in the forest shade; where evergreens prevail, the herbage always is exempt from direct insolation.

FIG. 86. — A colony of the bur-reed (*Sparganium eurycarpum*); the sunlight reaches the leaves at all depths, in spite of their dense arrangement; closely placed vertical leaves permit a maximum of lighting for vegetation as a whole, though the amount received by each leaf is relatively small; a water lily (*Castalia*) is seen in the foreground. Miller, Indiana. — Photograph by MEYERS.

Vertical leaves. — Some leaves (especially among xerophytes) are slightly if at all diaphototropic, assuming a vertical position through their growth activity. *Lactuca scariola*, for example, has diaphototropic leaves in the shade, but in the sunlight the leaves twist about into the *profile position* (fig. 88). In the compass plant (*Silphium*

laciniatum) and often in *Lactuca* the leaves not only are vertical, but also face east or west. In *Eucalyptus globulus* intense light induces not only a vertical instead of a horizontal position, but a change in leaf form as well. Such changes in reaction accompanying an increase of light intensity are not at all easy of explanation. Probably of similar import are the changes in orientation from the base to the apex in the leaves of many plants (as *Verbascum* or *Nicotiana*, fig. 89); the intermediate

FIG. 87. — A plant of wild spikenard (*Aralia racemosa*), displaying a kind of leafage common in rich mesophytic woods; note the large, compound diaphototropic leaves with broad leaflets, which are very thin and capable of enduring considerable shade; Manitou Island, Michigan. — Photograph by THOMPSON.

leaves show gradations between the large horizontal lower leaves and the small vertical upper leaves. The resultant plant contour is a cone, a shape well fitted for light reception. Probably such changes in leaf orientation are due partly to a change in the character of the phototropic reaction as the light becomes more intense; but other explanations are possible (p. 117), and cautious statement is necessary until more experimental data are available. In some plants the leaf position is determined by mechanical factors; for example, banana and palm leaves, though diaphototropic, often hang vertically because of their weight. Growing *Yucca* leaves tend toward

verticality, but crowding and other factors cause them to assume various positions.

The advantages of leaf reactions to light. — *Diaphototropic leaves.* — In the open, plants commonly receive much more light than they can use in carbohydrate synthesis, carbon dioxide and temperature being more important as limiting factors. But in the shade the amount of light may be insufficient, hence it follows that there the leaf arrangement is of high importance. Indeed, in dense cultures the lower leaves of many plants soon die, presumably from lack of light; the absence of leaves on the lower branches of forest trees doubtless has a like explanation. Experiments show that synthesis in a given leaf is reduced greatly when the incident light penetrates another leaf, and that it practically ceases if it penetrates two leaves. Hence the avoidance of shading through petiolar growth and otherwise is of great significance. Diaphototropism favors maximum light exposure, and its advantage is apparent. Less obvious is the advantage resulting from the facing of leaves toward light; in so far as the upper surface, regardless of exposure, has the maximum chlorenchyma development, the advantage is evident, but in a great many leaves (as in *Lactuca scariola*, *Populus deltoides*, and *Eucalyptus globulus*), the greatest development of the chlorenchyma occurs on whichever side is the more exposed to light. Surface expansion is almost universally characteristic of leaves, and though perhaps not caused by light, it is none the less of prime importance in light reception.

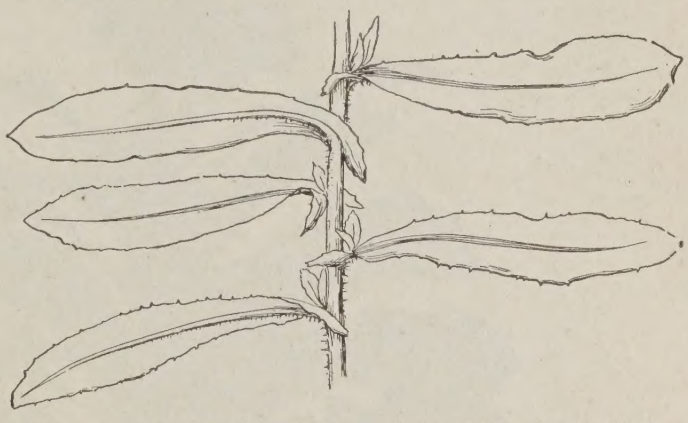


FIG. 88. — A portion of a sun plant of the prickly lettuce (*Lactuca scariola*), showing the characteristic twisted leaf bases and the resultant fixed vertical or profile position; occasionally, as here, the leaves are in one plane, facing east or west, as in the compass plant.

In most of the leaf forms above considered there is a tendency toward the display of a maximum surface to incident light. In vertical leaves and also in leafless stems the exact reverse occurs. In the latter the chief limiting factor is not insufficient light, but rather too great transpiration; perhaps, too, the excessive light may be

directly injurious to the chlorophyll and hence to synthesis. The peculiar reaction of the compass plant has been supposed to be par-

FIG. 89. — A plant (*Nicotiana alata*), illustrating a conical habit due to a decrease in the size and in the horizontality of the leaf blades from the base to the apex; note also that the leaves change in shape, being blunt below and pointed above, and that they are arranged in many vertical rows; this plant, like the mullein, illustrates a relative maximum of lighting coupled with a minimum of shading, and also a progressive increase from the base to the apex of features that protect from excessive transpiration. — Photograph by FULLER.

ticularly advantageous, since a leaf facing east or west misses the intense zenith rays and yet has the full benefit of the weaker rays of morning and evening. The situation in *Nicotiana* and *Verbascum* is

still more complicated, there being from the base to the apex a series of leaves varying in form and position in apparent correspondence with the increasing light intensity; the basal leaves seem fitted for maximum light reception, and the apical leaves for maximum light avoidance.

The position of leaves on stems. — Light reception is facilitated by various features of leaf structure and arrangement, which have little or no causal connection with light. While petioled leaves usually have considerable plasticity in their orientation and thus are relatively free from disadvantages due to place of origin, the particular orientation of sessile leaves often is determined by their stem position or *phyllotaxy*. Leaves usually are arranged in cycles (whorls) or in spirals. A simple and common arrangement, known as *decussate*, is that in which two-leaved cycles alternate with one another, resulting in four vertical rows (*orthostichies*) of leaves (fig. 83). There are many systems of spirals, the simplest being the *distichous* or $\frac{1}{2}$ arrangement (*i.e.* there are two orthostichies, one stem circuit making a complete round of the spiral; fig. 30). Progressively more complicated arrangements are $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, the latter meaning, for example, that there are thirteen orthostichies, and that five stem circuits are necessary for a complete round of the spiral, the fourteenth leaf being above the first, etc.

FIGS. 90, 91. — Experimental modification of the phyllotaxy in the luminous cave moss (*Schistostega osmundacea*): 90, a shoot which, after the development of ordinary distichous leaves (*l*), has been exposed to feeble illumination; the new leaf arrangement (*r*) is spiral; 91, a shoot which from the first has been exposed to feeble illumination, hence exhibiting spiral arrangement throughout. — From GOEBEL.

Spiral phyllotaxy is advantageous from the standpoint of leaf lighting, since it results in relative remoteness between the members of the same orthostichy; the screw pine (*Pandanus*) gives an admirable illustration of such arrangement, due to a high-ranked spiral. A relation sometimes is claimed to exist between phyllotaxy and leaf size, that is, complex spirals are supposed to be associated with small leaves and simple spirals with large leaves. Small leaves often occur in many ranks (as in *Yucca*, *Lycopodium*, and *Polytrichum*, fig. 207), and large leaves likewise; probably such relations are fortuitous. The causes of variations in phyllotaxy are not definitely known. A common theory has been that leaf position is due to mechanical influences exerted in the bud, such as the pressure of older parts upon those just developing; in recent years, however, many serious objections to this view have been advanced. The $\frac{1}{2}$ system that commonly

obtains in *Phyllocactus* is changed to a $\frac{1}{3}$ system when the plant is grown in the dark; similar changes have been observed in *Lycopodium* and in *Schistostega* (figs. 90, 91), and in *Caulerpa*, " leaves " occur only on the lighted side. In any case, no connection need be sought between the causes and the advantages of the various kinds of phyllotaxy.

Compound and small leaves. — Divided leaves, such as those of ferns (fig. 92), milfoils, and many water plants, are peculiarly favorable for light reception, because the sifting of the light between the leaf divisions enables it to impinge upon the leaves beneath. The aggregate surface exposed in a day is much greater than in a colony of plants with large simple leaves, because of the lighting at different

FIG. 92. — A mesophytic forest with a luxu ant undergrowth of ferns (*Osmunda*), whose compound leaves permit the sifting of light and the consequent illumination of subjacent foliage; Porter, Indiana. — Photograph by MEYERS.

levels, due to the shifting of the sun, and to the pliancy of the leaves in wind or water currents. Probably the amount of leaf surface lighted at any given moment is also greater than in the case of simple leaves, because of reflection from one leaf surface to another. Plants with numerous small leaves, such as pines and spruces, have the same general effect as do plants with divided leaves, and they exhibit the same sort of light-sifting. Probably the lower leaves of plants with divided or small leaves are less likely to suffer injury from shade than are similar leaves in sunflowers and in other plants with large entire leaves. In some plants (as *Monstera* and various oaks) the upper leaves are more divided than those beneath, thus facilitating light penetration; in quite as many plants, however, the lower leaves are more divided than the upper. There is no evidence in either case that light has any causal relation to leaf division; any advantage that may come in the way of light reception is to be regarded as purely incidental.

4. AIR CHAMBERS AND STOMATA

Gaseous exchanges in plants. — The chief gas movements in plants are associated with respiration, carbohydrate synthesis, and transpiration. Respiration, involving the absorption of oxygen and the emission of carbon dioxide, takes place in nearly all plants at all times, though it is slight, or even wanting, in "resting" organs, such as seeds. Carbohydrate synthesis, involving the absorption of carbon dioxide and the emission of oxygen, is confined essentially to chlorophyll-bearing organs in the presence of sunlight. Transpiration, involving the emission of water vapor (evaporation), occurs in all aerial organs, being absent in the water and slight in the ground or in very humid air. Transpiration involves much the greatest gas movement, respiration much the least. In the lowest plants, where each cell is in contact with the surrounding medium, there are few or no air cavities. In the higher plants, however, there are systems of connecting intercellular air chambers, communicating with the outside air by openings (such as stomata) or by loose external tissues (such as lenticels). Plants, therefore, have an internal atmosphere, differing somewhat from that outside, though tending to approach it by diffusion.

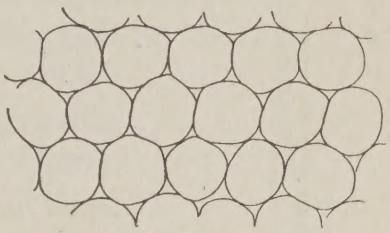


FIG. 93. — A tangential longitudinal section near the upper surface of a leaf of the century plant (*Agave americana*), showing palisade cells in cross section; note the small intercellular air spaces; highly magnified.

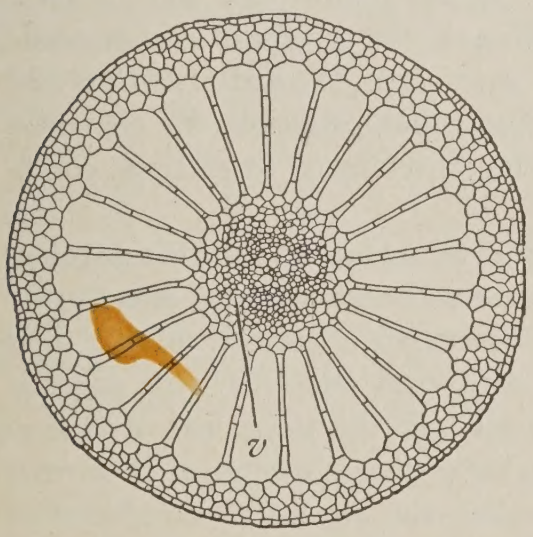


FIG. 94. — A cross section through the stem of a water milfoil (*Myriophyllum*), showing large and symmetrically arranged air chambers; note also the centrally placed conductive region (*v*), whose cells are relatively undifferentiated; considerably magnified.

The structural features and variations of air spaces. — The lower leaf chlorenchyma, the spongy tissue, is especially rich in *air spaces* or *lacunae* (figs. 61, 76, 126), and a rather prominent air cavity underlies each stoma. There are small intercellular spaces between all of the chlorenchyma

cells, those between the palisade cells being narrow and inconspicuous, except as seen in cross section (fig. 93). The thin cell walls adjoining the air spaces are of cellulose. *Air chambers*, often beautifully symmetrical in arrangement (as in the stem of *Myriophyllum*, fig. 94), are particularly conspicuous in hydrophytes, where they occur in all the vegetative organs, their total volume often being greater than that of the cells. In submersed leaves the entire mesophyll consists of spongy parenchyma with large lacunae (fig. 325), while in floating leaves there may be a striking contrast between the emersed palisade layer and the submersed sponge (fig. 109). Sometimes, as in the leaf of *Juncus* (fig. 95) and in the stem of *Zizania*, large air chambers are partitioned off by *diaphragms*, which often appear to the naked eye as cell walls. Air chambers are said to be less abundant in plants of swift streams than in those of ponds and swamps. Xerophytes, particularly succulent species, are characterized by small and inconspicuous air spaces (figs. 141, 232). Alpine plants are said to have smaller lacunae than do the otherwise similar arctic plants. In some cases, as in the leaf of *Allium* and in the stem of *Equisetum*, capacious air chambers develop without much reference to external conditions (fig. 335).

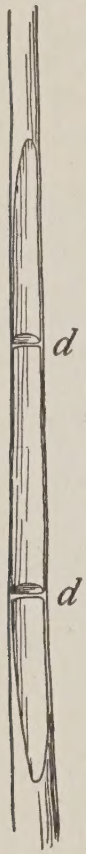


FIG. 95. — A part of a leaf of *Juncus nodosus* with a portion cut away, disclosing capacious air chambers, separated from each other by horizontal plates, the diaphragms (*d*).

The influence of external factors upon the development of air spaces. — *The plasticity of lacunar tissues.* — Lacunar tissues are extremely plastic, and commonly have reciprocal relations with palisade tissues. For example, in the water leaf of *Proserpinaca*, the entire mesophyll is composed of lacunar tissue (fig. 70), while the air leaf is composed of palisades above and of lacunar tissue below (fig. 69). In *Lactuca scariola* there are possible all variations from a mesophyll composed entirely of sponge to a mesophyll composed essentially of palisades (figs. 71, 72). When the phellogen or cork cambium (p. 220) of certain swamp plants (as *Jussiaea* and *Decodon*) is submerged, it develops into a loose lacunar tissue, known as *aerenchyma* (fig. 96), whereas in the air it develops into cork. In each case the mature

tissue is made up of cells arranged in radial rows, but in aerenchyma capacious air spaces are interspersed regularly, while cork is remarkably free therefrom. Furthermore, in the aerenchyma the cell walls are thin and of cellulose. The great development of air spaces gives the stem a swollen appearance, and frequently the aerenchyma grows so rapidly as to break through the bark, forming whitish patches; the so-called water lenticels are similar scattered patches of whitish tissue, formed under identical conditions (p. 179).

The factors involved. — The exact factors causing the development of lacunar tissue are not known, though it is evident that the dominating influence is external. The essential feature to be explained is the development of lacunae, since the cell shape may remain much as in embryonic tissue, contrasting with the great change in cell shape without conspicuous lacunar development in the palisade layers. Two theories have been suggested, one that lacunae are a reaction to low oxygen pressures, the other that they are developed where transpiration is weak. The oxygen theory has been employed only in connection with the great development of lacunae in water plants, especially where aerenchyma is formed. The evidence for this theory is slight; differences in oxygen pressure quite fail to account for the sudden change from lacunar to compact tissue at the water line (as in the leaf of *Nymphaea* and in stems with aerenchyma). Almost without exception lacunae vary inversely with the transpiration, the largest air chambers being in the water where transpiration is reduced to zero. Elsewhere palisades have been seen to vary directly with the transpiration, so that the causative factors of reciprocal leaf structures themselves appear to be reciprocal. The mechanics of the process, that is, the exact method whereby the reduction of transpiration influences tissues so as to produce large air spaces, is for the present scarcely to be conjectured.

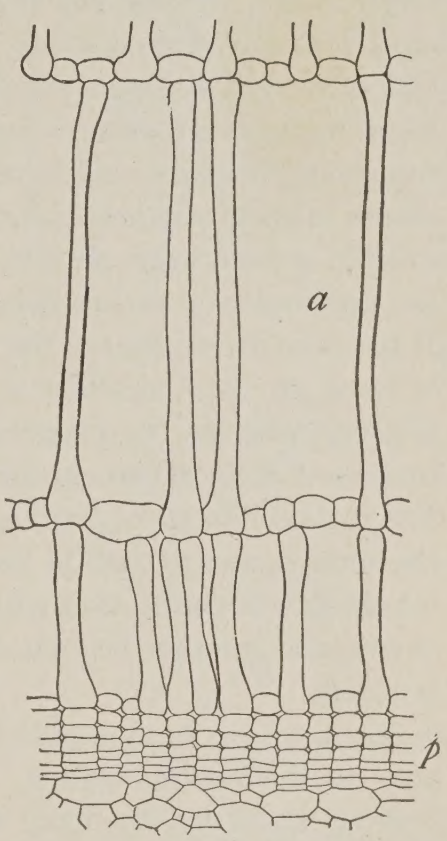


FIG. 96. — A cross section of the submersed part of a stem of *Jussiaea peruviana*, showing the development of aerenchyma (*a*) from phellogen (*p*); note the capacious air spaces; highly magnified. — From SCHENCK.

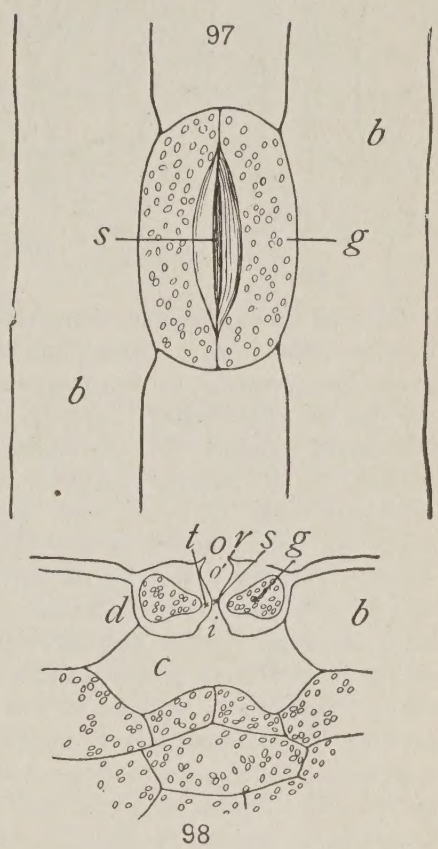
The rôle of air spaces. — *Air reservoirs.* — Air spaces are of vital importance in furnishing ready ingress and egress for oxygen and carbon dioxide to and from the active cells of the leaf chlorenchyma in connec-

tion with respiration and carbohydrate synthesis; these spaces also greatly facilitate transpiration, the significance of which is to be considered elsewhere. In ordinary lakes and ponds, oxygen and carbon dioxide are comparatively abundant, hence the large air spaces there appear to be without advantage, so far as aeration is concerned, unless the absence of stomata makes the entrance and the exit of gases relatively slow. In stagnant swamps and undrained ponds, however, the oxygen supply often is scant; indeed, it is commonly believed that the lack of oxygen accounts for the quick decay of algae when transferred from running streams to standing water. In such habitats, then, capacious air spaces may be of much value as oxygen reservoirs. Green plants in their synthetic processes give off much more oxygen than is utilized in respiration, so that the presence of large air chambers permits the accumulation rather than the complete dispersion of this oxygen. It has been shown that in the water lilies the maximum oxygen content of these air chambers is at sunset, at the close of a day of synthetic activity, whereas the maximum for carbon dioxide occurs at sunrise, by reason of the accumulation of the products of nocturnal respiration. The carbon dioxide utilized in synthesis probably is more abundant in the average waters than in the air, so that air reservoirs are of doubtful efficacy in connection with that process. Furthermore, in aerenchyma and in other lacunar tissues in many hydrophytes chlorophyll is absent.

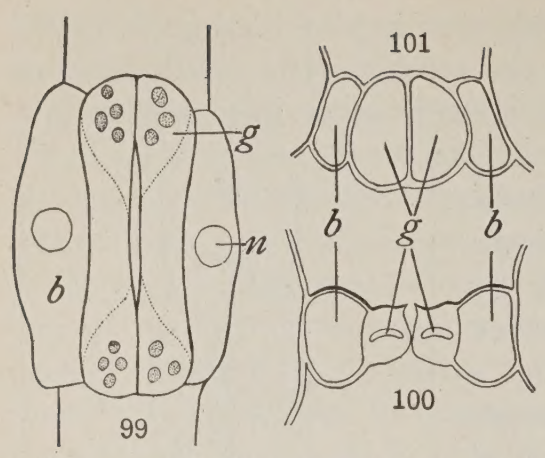
Buoyancy. — In most water plants air chambers serve to give buoyancy to the various organs. The position assumed in the water by floating leaves and by many submersed and emersed leaves and stems is determined by the volume of their air spaces; for example, the distended petioles of the water hyacinth make the plant so light that it floats with its leaves high above the water. The air-containing *bladders* of various marine algae (as *Fucus* and *Nereocystis*, fig. 52) serve to keep these plants at levels favorable for synthetic activity during periods of high tide. Some fresh-water algae (as *Cladophora* and *Spirogyra*) are floated near the water surface by bubbles of gas, which become entangled among the filaments. *Ceratophyllum*, though usually not attached, stands vertically in the water by reason of the difference in specific gravity between the stem and the leaves, the latter being rich in air spaces. During the autumn the winter buds of duckweeds and bladderworts (figs. 306, 307), which are heavier than water, become detached from the floating plant body, and sink to the

bottom of the pond; in the following spring these buds grow, developing large air spaces which lessen the specific gravity sufficiently to enable them to come again to the surface, where they develop into ordinary vegetative shoots.

The structure of stomata. — The air chambers of leaves and of young stems communicate with the outside air by means of *stomata;* as seen in surface view, these organs consist usually of a narrow slit, the *stoma proper* (though the apparatus as a whole often is called a stoma), flanked by two kidney-shaped *guard cells* in contact at the ends but separated along the middle (fig. 97). Usually the guard cells are adjoined or surrounded by *subsidiary cells* (figs. 99–101), which sometimes differ from the other epidermal cells. Most guard cells differ from the adjoining epidermal cells in possessing chloroplasts, starch grains, and abundant cytoplasm with a prominent nucleus. In cross section (fig. 98) the guard cells reveal some complexity of structure. Toward the ventral (slit) side, the upper parts of the walls project in sharp cutinized *ridges* that almost meet when the stoma is closed. In most cases the corresponding lower walls project similarly but less prominently, and the space between them is greater. In the median region is a third but rounded pair of projections with slightly thickened walls; since stomatal closure is effected by the meeting of these median projections, the very narrow slit between them (known as the *central slit*) might properly be regarded as the true stoma. The narrow spaces between the ridges



FIGS. 97, 98. — Stomata from the leaf of an Easter lily (*Lilium longiflorum*): 97, a stoma, as seen in surface view, showing the two kidney-shaped guard cells (*g*), which enclose the stomatal aperture (*s*), the more deeply shaded portion representing the central slit; note the chloroplasts in the guard cells; *b*, subsidiary cells; 98, a stoma, as seen in cross section; the wall of the guard cell (*g*) next to the subsidiary cell (*b*) is the dorsal wall (*d*), the wall next to the central slit (*s*) being the ventral wall (*t*); the outer slit (*o*) is enclosed between the cutinized outer guard-cell ridges (*r*), the enlarged area just below being the outer vestibule (*o'*); below the central slit is the inner vestibule (*i*), which here opens directly into the stomatal cavity (*c*); highly magnified.



FIGS. 99–101. — Stomata from the leaf of a grass (*Poa*): 99, a stoma from the blue grass (*Poa pratensis*), as seen in surface view, showing the guard cells (*g*) with their dumb-bell-shaped lumina, the chloroplasts being confined to the enlarged portions; note the subsidiary cells (*b*) with their prominent nuclei (*n*); 100, a median cross section of the stoma of *Poa annua*, showing the narrow portion of the guard-cell lumina (*g*) and the relatively large median portion of the subsidiary cells (*b*); 101, a cross section through the end portion of the stoma of *Poa annua*, showing the enlarged part of the guard-cell lumina (*g*), the terminal portion of the subsidiary cells (*b*) being relatively small; highly magnified. — 100 and 101 from HABERLANDT.

above and below are known, respectively, as the *outer* and the *inner slits* or openings, while the larger spaces separating them from the central slit are the *outer* and the *inner vestibules*. The *dorsal walls* are of cellulose and are much thinner than are the *ventral walls;* frequently they are connected with the subsidiary cells in such a way that the walls of the latter may swing back and forth like hinges, moving the guard cells with them (figs. 103, 110). Below the stoma is a rather large *air cavity*.

Structural variations of stomata. — *Taxonomic variations.* — Many stomatal variations have no obvious relation to external conditions, as in grasses and conifers, where a certain structural plan appears to characterize an entire family, regardless of environment. In grasses (figs. 99–101) there are large sub-

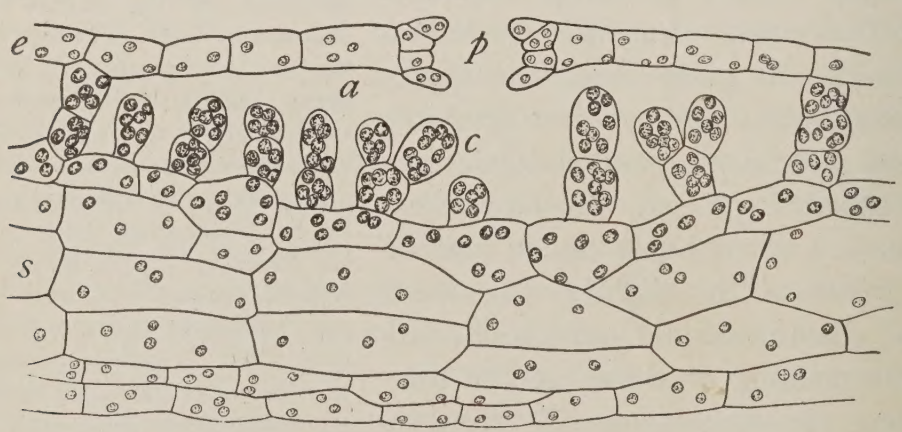


FIG. 102. — A section through the thallus of *Marchantia polymorpha*, showing an air chamber (*a*), an air pore (*p*) with its surrounding cells, the chlorenchyma composed of short alga-like filaments (*c*), and a tissue of closely packed cells (*s*) in which the chloroplasts are sparse; the latter tissue is rich in water; highly magnified. — From COULTER (Vol. One).

sidiary cells behind the dumbbell-shaped guard cells. The corn plant possesses such stomata except within the sheathing portions of its leaves where the lily type (fig. 97) is often found. In plants with scapose stems the stomata on the scapes often differ somewhat in form from those on the leaves. The sporophytes of mosses and of *Anthoceros* have stomata much like those of higher plants, except that the inner cutin ridges usually are wanting and that the guard cells vary in number from one to four. In the gametophytes of the Marchantiaceae there are capacious air chambers, which communicate with the exterior through simple *air pores* that sometimes are enclosed by chimney-like tiers of cells (as in *Marchantia*, fig. 102).

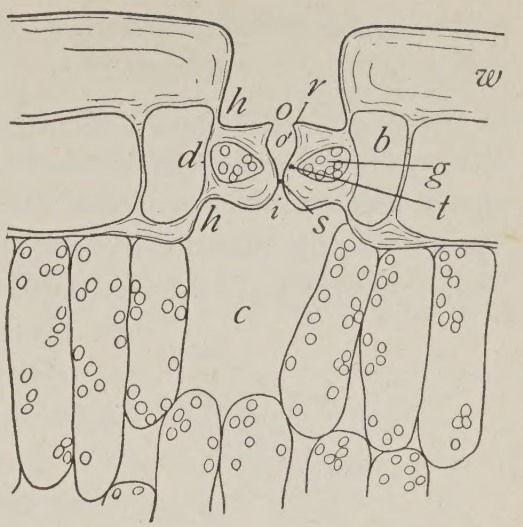


FIG. 103. — A cross section through a stoma from a leaf of the carnation (*Dianthus caryophyllus*); by reason of the heavy cutinization of the outer epidermal wall (*w*), the stoma lies below the surface level of the leaf; note the thin places (*h*) above and below the dorsal wall (*d*) of the guard cell (*g*), representing the so-called hinges which are thought to facilitate guard-cell movement; the chamber above the stoma is called a stomatal pit; general lettering as in fig. 98; highly magnified.

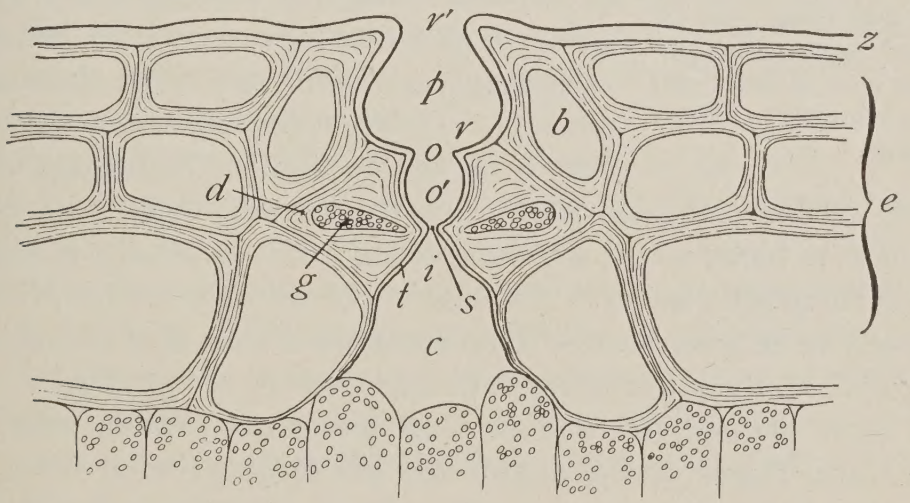


FIG. 104. — A cross section through a stoma from a leaf of the India-rubber tree (*Ficus elastica*); the stoma lies below the surface level of the leaf by reason of its position beneath the subsidiary cells (*b*), which have projecting ridges (*r'*) partially enclosing the pit (*p*); the dorsal wall (*d*) of the guard cell is so braced by the thick walls of the adjoining cells that guard-cell movement must be slight; note that the epidermis (*e*) consists of three cell layers and that the cuticle (*z*) is highly developed; general lettering as in Fig. 98; highly magnified.

Variations associated with habitat. — In many xerophytes the stomata occur in pits; sometimes, as in *Dianthus* (fig. 103), there is one stoma at the base of each pit, while in other cases (*Nerium*, *Begonia*) the stomata occur in groups. In *Populus pyramidalis* the pits of the upper leaf surface are deeper than are those of the lower. In most xerophytes the guard cell walls are very heavily cutinized (fig. 104); sometimes the walls are thickened uniformly, but more frequently there are projecting ridges of remarkable shapes and dimensions. In *Nipa fruticans*, for example, the ventral walls project in such a way as to form a most tortuous passageway between the leaf interior and the outside air (fig. 105). Both in heavy cutinization and in depression below the surface level, the stomata of conifers agree with those of many xerophytes, and are, perhaps, to be regarded as xerophytic stomata. The stoma-bearing under surface of xerophytic leaves is often hairy, contrasting with the smooth upper surface (as in *Antennaria* or in *Populus alba*, fig. 126), while in other cases hairs may develop only in pits (as in *Nerium*, fig. 113) or in furrows. Similarly, wax deposits often are observed on stoma-bearing surfaces, and waxy or resinous excretions may even clog up the stomata. Occasionally intrusive growths, known as *tyloses*, due to the bulging of adjoining cells into the stomatal air cavity, develop to such an extent as almost to block up the air passages (fig. 106); especially is this the case in xerophytic leaves. The stomata of vernal herbs (as *Medeola*) are likely to be less protected than are those of trees or of estival herbs (as *Achillea*), the latter being more like those of xerophytes.

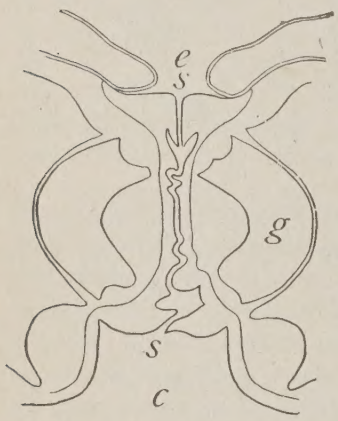


FIG. 105. — A cross section through a stoma from the under leaf surface of the nipa palm (*Nipa fruticans*), showing the tortuous passageway (*ss*), which must be traversed by transpiring water that passes from the stomatal cavity (*c*) to the exterior at *e*; *g*, guard cell; highly magnified. — From BOBISUT.

In most hydrophytes and in some mesophytes (as in ferns) the inner cutin ridges of the guard cells are lacking; in a few cases, even the median ridges are absent. Rarely, except in some hydrophytes, are the stomata lifted above the epidermal level. The stomata of cotyledons are relatively uniform in structure, thus seeming to correspond with the uniform conditions under which cotyledons are developed.

The influence of external factors upon the structure of stomata. — A slight decrease in the size of the guard cells and a slight increase in the cutinization of their walls, when developing stomata are exposed to dry air or to other xerophytic conditions, are about the only changes that have been experimentally induced in the structure of stomata, a fact that seems remarkable in the light of the extreme plasticity of other superficial cells and tissues. The extensive habitat variations above noted make the structural rigidity of stomata all the more extraordinary. As appears from the following paragraphs, stomata often can be induced or inhibited at will, but their structure, when present, seems fixed; however, the paucity of experimental data makes any general conclusion hazardous.

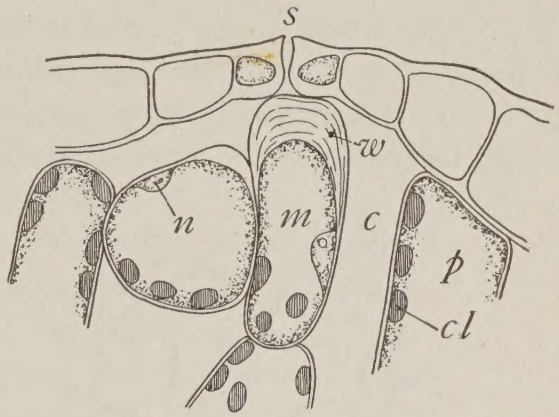


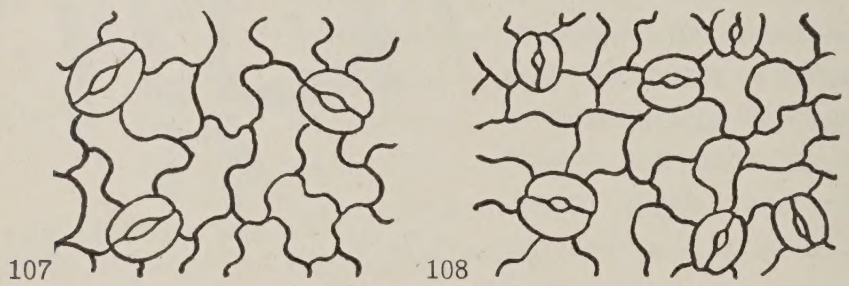
FIG. 106. — A cross section through a stoma from the upper leaf surface of *Pilea elegans*, showing the closure of the stomatal passageway by the protrusion of a mesophyll cell (*m*) into the stomatal cavity (*c*); such outgrowths are known as tyloses; note the great thickening of the wall (*w*) just beneath the stoma; *s*, guard cells; *p*, chlorenchyma cells with chloroplasts (*cl*) and nuclei (*n*); highly magnified. — From HABERLANDT.

The arrangement of stomata. — As a rule, stomata overlie the mesophyll rather than the veins, and commonly they number from 100 to 400 per square millimeter, although sometimes as many as 1000 per square millimeter have been found. In most monocotyl leaves the stomata are in longitudinal rows and have a common orientation, their long axes coinciding with that of the leaf. In most dicotyl leaves the somewhat more numerous stomata are scattered irregularly and their long axes are oriented in various directions (fig. 108). In some broad monocotyl leaves the stomata are arranged and oriented irregularly, while in many narrow dicotyl leaves they occur in rows, thus suggesting that leaf shape and venation rather than systematic position may be the chief determining factors; in *Salsola* and in some other halophytes the stomata are in rows and are transversely oriented; in *Saxifraga granulata* the broad basal leaves exhibit irregular orientation, while the narrow upper leaves have the regular orientation characteristic of monocotyls.

It has been shown that stomata become decidedly more numerous per unit area the higher up on the stems the leaves are inserted and that this is so regardless of the size of the leaf blades. The stomata and epidermal cells of the upper leaves, however, are decidedly

smaller than those of the lower leaves. Thus on an upright flowering shoot of *Spiraea* the lowest four leaves had an average of 320 stomata per square millimeter, the four leaves next higher up on the stem had 390 stomata, and the six leaves still higher up had more than 500 stomata per square millimeter (figs. 107, 108).

The leaves of most trees, whether mesophytic or xerophytic, are without stomata on the upper surface; in *Juniperus* the stomata are confined to the upper surface, but that is the least exposed surface during the winter (p. 97); in *Populus deltoides* the stomata are about equally abundant on the two surfaces while in *Populus tremuloides* they are confined to the under surface, and yet in both species the constant trembling of the leaves frequently exposes the under side to the



FIGS. 107, 108. — Lower epidermis, with stomata, from leaves of spiraea (*Spiraea ul maria*); Fig. 107 from the second leaf from the ground and Fig. 108 from the tenth leaf of the same erect shoot; magnification the same for both. — After YAPP.

sun. In grasses the stomata usually are confined to the upper surface, which is the more protected side in dry weather, owing to the infolding of the leaves (figs. 141–143). Except in a few instances submersed hydrophytes are without stomata, so that their large air chambers have no direct outside connection. In floating foliage organs, such as water lily leaves (fig. 109) and duckweeds, the submersed under surface is without stomata, while they are abundant on the emersed upper surface; the submersed leaves of water lilies are quite without stomata. Subterranean organs have no stomata, as a rule, though the latter are present in some instances. Most xerophytes have few or no stomata on the upper leaf surface, though various conifers (as *Juniperus*) and most Crassulaceae have numerous stomata on that side.

The influence of external factors upon the development and arrangement of stomata. — *The variations.* — Xerophytic leaves, though often smaller than the mesophytic leaves of the same species, usually have smaller epidermal cells and more stomata per unit area. Such an increase in the number of stomata within a species is to be regarded

as a xeromorphic character whether it results from dry air or from dry soil. In some plants (as *Asperula tinctoria*) the orientation of stomata varies with the habitat, mesophytic individuals exhibiting irregular orientation, while xerophytic individuals exhibit longitudinal orientation as do monocotyls. The most pronounced influence of external factors is found in amphibious plants, where stomata ordinarily can be induced or inhibited at will by growing the plants respectively in air or in water. Stomata occur on both surfaces in the air leaves, but on the upper surface only in the floating leaves of *Polygonum amphibium* and *Ranunculus sceleratus*, the air leaves of the latter having more stomata on the upper surface in moist air and on the under surface in dry air. Whatever the conditions of germination, the first leaves of *Proserpinaca* have stomata, but they originate within the seed in contact with air instead of with water; subsequent submersed leaves have no stomata, whereas emersed leaves have them in abundance (figs. 69, 70). Subterranean scale leaves usually have no stomata, yet when the primordia of such leaves are exposed to light and air, they often develop into foliage leaves with abundant stomata, while the primordia of foliage leaves when grown in the soil become scale leaves and are devoid of stomata. Sometimes stomatal development begins in the soil, but it is completed only in the light and air.

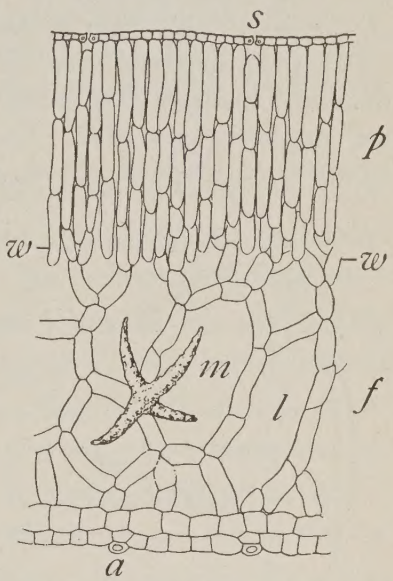


FIG. 109. — A cross section through a leaf of the yellow water lily (*Nymphaea advena*), showing a strong development of palisade tissue (*p*) in the upper half which is above the water level (*w*), and an unusually loose spongy tissue with large lacunae (*l*) in the lower half which is below the water level; the stomata (*s*) are confined to the upper surface; *a*, slime gland; *m*, stellate stereid; considerably magnified.

The factors involved. — The factors that induce the appearance of stomata are not known, though in most instances air is a necessary medium for their development. It has not been ascertained which element of the air is the most important, nor what is the nature of its influence. There is some evidence also that light tends to favor the development of stomata. Since stomatal activity is confined to the air, it is possible that there is some relation between gas exchange and stomatal development. In particular, stomata are abundant where transpiration is vigorous, and absent where it is reduced or wanting.

The mechanism of stoma movement. — Guard-cell movements are extremely complex and not clearly understood, while their amount and importance often are overestimated. They are best illustrated in mesophytes, the stomata of most xerophytes being generally in a state of partial closure, while those of hydrophytes and of plants with motile leaves, as well as the air pores of liverworts, generally are open; even in mesophytes, closure by no means implies hermetic sealing. The guard cells, as compared with other epidermal cells, are vigorous and active, living even for weeks when removed from the leaf and placed in a nutrient medium; they are unusually resistant also to high temperatures and to other factors which generally are harmful to plant cells. The opening of stomata in moist air is thought to be due to the distention of the guard cells when they absorb a large amount of water. The

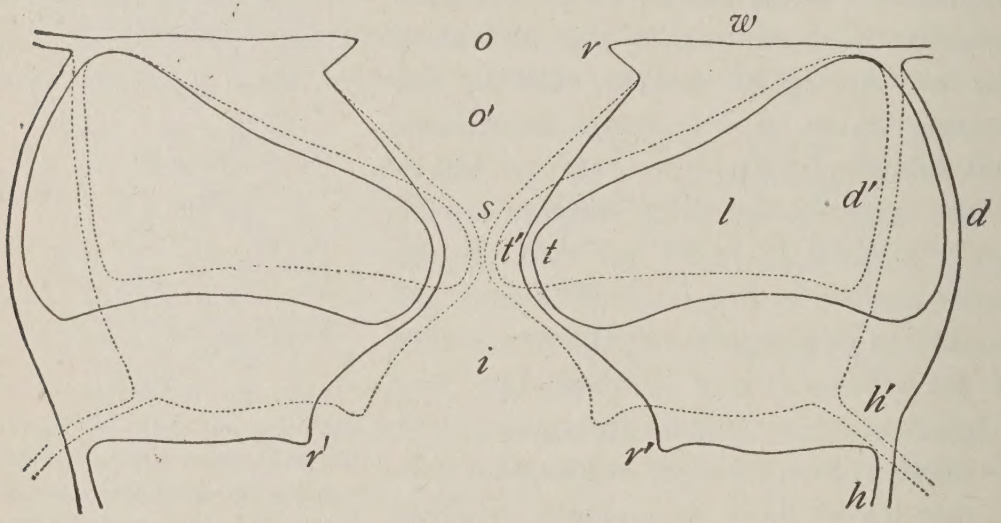


FIG. 110. — A diagrammatic cross section through a stoma of *Helleborus*, illustrating guard cell movement; the solid lines represent the open position and the dotted lines the closed position; closure involves the movement toward the central slit (*s*) of the ventral wall (*t*) and the dorsal wall (*d*), these walls assuming the positions, *t'* and *d'*, respectively; the hinge (*h*) moves in the same direction, assuming the position, *h'*; the outer walls (*w*) remain immobile; the movements of the ventral and the dorsal walls decrease the sphericity of the cell lumen (*l*); *r'*, inner ridges; general lettering as in fig. 98; highly magnified. — From SCHWENDENER.

resulting approach toward sphericity in the guard cells and the stretching of their thin dorsal walls, often supplemented by the action of hinge walls in the subsidiary cells, cause the withdrawal of the median ridges and the consequent opening of the central slit (fig. 110). Exposure to dry air is thought to lessen the distention, whereupon the guard cells swing back to a position of closure. In grasses stomatal opening is effected by the mutual pressure of the dumbbell-shaped ends of the guard cells, supplemented by the *buffer cells* at each end, which resist longitudinal distention (fig. 99).

The causes of the nocturnal closing and of the diurnal opening of stomata are imperfectly understood, though there is evidence to show that the movements are due to varying turgor in the guard cells due to the transformation of their contained food materials. Enzymatic activity effecting these transformations seems to be dependent upon light conditions. Three main groups of plants have been

recognized with somewhat different stomatal behavior. The first group includes the cereals in which the stomata, under ordinary conditions are always closed at night. They open during the day, the period of opening being reduced by a deficiency of moisture. The second group embraces most thin-leaved mesophytes such as alfalfa (*Medicago sativa*). Under favorable circumstances their stomata behave like those of the first group but under conditions of great heat and dryness they are closed all day and open all night. A third group includes the potato and most plants with fleshy leaves whose stomata, under favorable conditions, are open both day and night. Under conditions of great dryness the stomata close during the day, opening again at night.

The rôle of stomata. — *Synthetic and respiratory exchanges.* — The chief advantage of stomata to plants is the facilitation of gas exchange in connection with carbohydrate synthesis. Experiments have shown that synthetic activity is much reduced if the stomata are artificially closed, as when the stoma-bearing under surface of a *Ficus* leaf is coated with wax. When the upper surface of such a leaf is slit, starch accumulates in the cells adjoining the incision, indicating the resumption of vigorous synthetic activity, and doubtless betokening the free entrance of carbon dioxide and the exit of oxygen. Small as are the stomatal openings and slight as is their aggregate surface, the intake of carbon dioxide by an ordinary leaf approaches the rapidity with which this gas is absorbed by a free surface of caustic alkali. Indeed, stomata might often be considerably fewer or smaller than they are without appreciably reducing the rate of gas exchange. Respiratory gas exchanges are so slow and involve so little oxygen and carbon dioxide that stomata are of minor significance therewith, although the gases involved doubtless pass through the stomatal passageways. Much the greatest movement of gas through the stomatal openings is the outward movement of water vapor, known as transpiration, a process that varies with the saturation deficit of the external atmosphere.

Functionless stomata. — Stomata in all stages of imperfect development are to be found on subterranean organs, on various parts of flowers, and on certain submersed leaves as well as on plants without chlorophyll.

5. PROTECTION FROM EXCESSIVE TRANSPIRATION

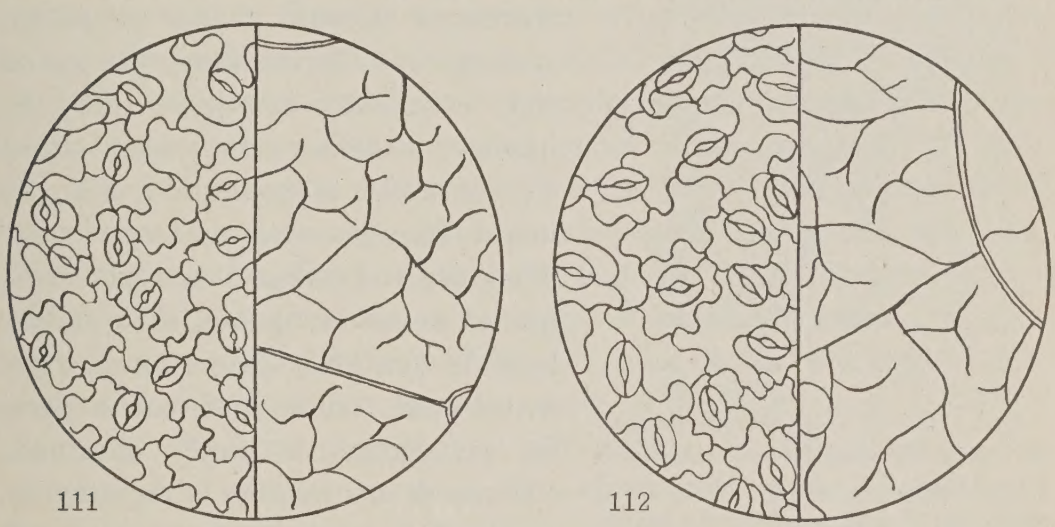
The significance of transpiration. — *The importance of water.* — Water plays a dominant part in the life of plants, being the most important single factor in determining the varying vegetation of ponds, deserts, meadows, rock cliffs, and of many other habitats. Water

forms a large part of the raw material from which plants build up foods and tissues, and all plant activity depends upon its presence in considerable amount in the cell sap. Although there is great and continual use of water, and although the supply frequently is inadequate, there is an enormous and increasing loss by transpiration. A large alfalfa plant may have more than a square meter of leaf surface and from each square meter of leaf surface the alfalfa often transpires from 200 to 300 grams of water per hour on a hot summer day. For every gram of dry matter produced a corn plant transpires from 300 to 400 grams of water, a wheat plant from 400 to 600 grams, and an alfalfa plant from 800 to 1000 grams; hence an acre of alfalfa, producing two tons of dry alfalfa hay, will have used during the season from 1600 to 2000 tons of water.

Transpiration and the absorption of salts. — Sometimes it is held that all plant activities necessarily are beneficial, else they would have been lost in the progress of evolution. Hence, various attempts have been made to discover the advantage of transpiration. The chief theory has been that, by accelerating the movement of water through plants, transpiration increases the amount of available mineral salts, since they enter and traverse plant tissues in solution in the water. This theory is not tenable, inasmuch as salts are not swept along in the water, but enter plants and move from cell to cell independently of one another and of the rate of movement of the water. The rate of entrance of a salt depends usually upon the rate at which it is utilized within the plant, since it moves from a place of high to one of low concentration. Within the dead conductive vessels a rapid movement of the water may facilitate the movement of salts, but no such phenomenon can occur in the living cells of the roots and leaves (see p. 208). Furthermore, this theory greatly exaggerates the amount of mineral salts used in plant growth. They are necessary only in very small amounts and are readily obtainable. The most luxuriant vegetation known is that of the humid tropical forests, where transpiration often is very slight (sometimes being almost negligible for days at a time), and there is no transpiration in submersed vegetation; yet in neither of these instances do the plants suffer from a lack of salts. Indeed, vegetative luxuriance varies inversely rather than directly with the transpiration.

The possible advantages and the certain disadvantages of transpiration. — The most probable advantage associated with transpiration is in those plants which have a high turgor pressure (Vol. Two, p. 81),

where it is a means of escape for an excess of water, the injection of air spaces thus being prevented. It has been claimed also that, in sunshine, transpiration occasions a constant water renewal, which serves to keep the leaf temperature near the optimum; leaves exposed to sunshine in saturated air may be a few degrees warmer than are freely transpiring leaves. These and other advantages, however, are to be regarded as incidental. Except in water and in saturated air, transpiration is a necessary companion of carbohydrate synthesis, since the very features (thin expanded leaves, numerous open stomata, capacious air spaces) that facilitate the latter also facilitate the former. One might conceive a leaf so fashioned as to inhibit transpiration,



FIGS. 111, 112. — The structure of bean leaves; 111 from a leaf of a plant grown in a drier and 112 from a plant grown in a moister atmosphere; the right of the circle showing the veins and the left the lower epidermis with stomata; equally magnified. — After MAXIMOV.

but such a structure would be valueless in synthesis. Transpiration, then, is necessary, whether or not it is, as sometimes is believed, a necessary evil. Excessive transpiration is the greatest danger to which plants are exposed, and the harm that it entails certainly far exceeds any incidental good.

Transpiration and xeromorphic leaf structure. — When the leaves of a plant develop under conditions that tend to increase transpiration, whether it be in an atmosphere of lower humidity or in more intense sunlight or at higher levels on the stem, they often are changed in structure. Such leaves should be termed *xeromorphic* rather than xerophytic. Xeromorphic leaves (excluding succulents) are characterized by such structures as greater length of veinlets per unit area (figs. 111, 112), smaller cells in upper and lower epidermis, more stomata per unit

area, thicker walls of epidermal cells with more cutinization, more palisade and less spongy chlorenchyma, and more mechanical tissue. Such xeromorphic leaves, however, usually are found to possess higher transpiration capacity, with actually higher rates of water loss per unit area, a higher rate of carbohydrate synthesis, and yet they are more drought resistant. It is becoming more and more evident that drought resistance results quite as much from the nature of the cell contents as from the structure of the leaf tissues.

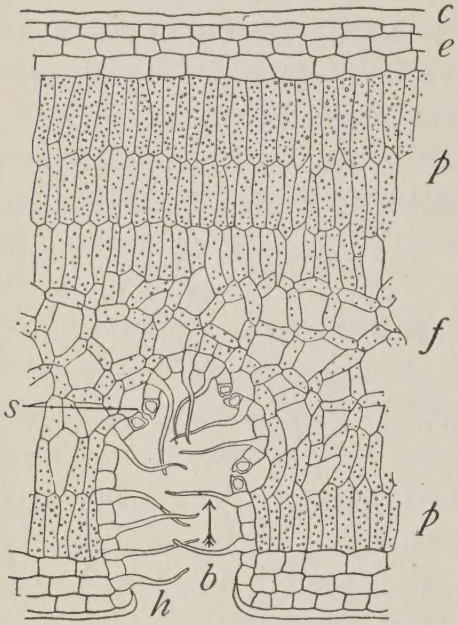


FIG. 113. — A cross section through the leaf of the oleander (*Nerium oleander*), showing a thick three-layered epidermis (*e*) with a prominent cuticle (*c*), a striking development of palisade tissue (*p*) below as well as above, a layer of sponge tissue (*f*) near the center instead of near the lower epidermis, and a stomatal pit (*b*) with stomata (*s*) that are slightly elevated above the level of the pit epidermis and with protective epidermal hairs (*h*); considerably magnified.

The protective structures and activities of stomata. — *The advantage of closure.* — The movements of guard cells commonly are interpreted as having protective significance, since, were it not for transpiration, stomata might remain open without harm. The closure of stomata by night is regarded as advantageous, since carbohydrate synthesis ceases upon light withdrawal, while sufficient oxygen for respiration is easily obtained. Closure in dry weather is regarded as useful, since at such a time it is much more important that the water supply be conserved than that synthetic activity be continued. In winter, when synthesis is slight, closure is beneficial because transpiration is particularly harmful by reason of diminished absorption.

Protective stomatal structures. — Doubtless transpiration is reduced by various stomatal structures, such as guard-cell cutinization, hairs, wax and resin deposits, and tyloses. The frequent restriction of stomata to the under leaf surface probably has a similar effect. Of importance, too, are pits, long or tortuous passageways, and alternations of cutin ridges with vestibules, all of which doubtless retard outgoing water. But stomatal structures and activities cannot stop transpiration; at best there is only retardation.

The advantages and disadvantages of stomata. — The great advantage of stomata is the facilitation of synthesis, and their great disadvantage the facilitation of transpiration. Stomata are most necessary where they entail the most harm, namely, in xerophytes, where the heavy cutinization makes the absorption of carbon dioxide through the cuticle almost impossible. Where stomata entail no danger, as in submersed hydrophytes, they are unnecessary, since gases pass readily through the non-cutinized epidermis.

The epidermis. — *General features.* — The leaf *epidermis* consists commonly of a single layer of cells (figs. 61, 62, 232), or sometimes of two or more such layers (as in *Nerium*, fig. 113; also figs. 67, 104), so compactly placed that no spaces intervene, except where stomata occur. On both leaf surfaces in submersed plants (figs. 64, 325), and often on the upper leaf surfaces in mesophytes and in xerophytes, there are no breaks whatever in the epidermis, which thus contrast strikingly with the chlorenchyma. In most dicotyls the cells are nearly isodiametric (figs. 117, 118, 217), while in monocotyls they usually are elongated in the same direction as is the leaf (fig. 99). Commonly the epidermal cells of air leaves differ from the mesophyll cells in the absence of chlorophyll (except in the guard cells) and in the presence of a cutinized outer layer, the cuticle; such an epidermis soon ceases to have any rôle other than that of protection. In submersed plants, however, the epidermis contains chlorophyll and remains uncutinized, thus taking part in absorption and in synthesis. The epidermal cells of hydrophytes and of mesophytes usually are larger than are like cells in xerophytes, and the growth of mesophytes in xerophytic conditions commonly results in a decreased cell size.

The outer epidermal walls; cutinization. — The outer wall of the epidermis, originally thin, and also permeable because composed of cellulose, in the adult leaf commonly is thickened through the deposition of *cutin*, a fatty substance highly impermeable to water. Usually the cutinized portion forms a continuous yellowish coat, the *cuticle* (figs. 113, 116), below which is the slightly modified cellulose portion of the outer wall. In some xerophytes a *cuticular layer* is interposed between the cellulose and the cuticle, the wall thickening progressively inward before it becomes cutinized (fig. 114). In *Pinus* the encroaching wall finally fills the entire lumen (fig. 346). In the grasses and in *Equisetum*, in addition to cutin, silica is deposited in the cell walls. Highly cutinized walls are characteristic of xerophytes, and particularly

of evergreen xerophytes, such as conifers, ericads, and many broad-leaved trees of warm temperate regions, for example, the live oak and the olive. Heavy cutinization characterizes many alpine and arctic plants, and also plants of peat bogs (as *Ledum*, *Andromeda*, *Chamaedaphne*) and of tropical salt marshes (as the mangroves); even mesophytic evergreens, as the yew and the hemlock, may have a prominent cuticle. Many succulent xerophytes, such as *Sedum* and *Salsola*, have a very weak development of cutin. Submersed plants, both in fresh and in salt water, commonly are free from cutinization.

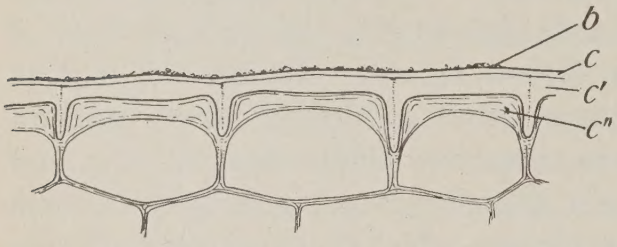


FIG. 114. — A cross section through the leaf epidermis of the century plant (*Agave americana*), showing the cellulose layer (*c''*), the cuticular layer (*c'*), the cuticle (*c*), and a superficial layer of wax grains (*b*) which constitute a glaucous bloom; highly magnified.

The influence of external factors upon cutinization. — No plant structure reacts more readily to changes in conditions than does the cuticle, submergence in water inhibiting its formation, and desiccation favoring its maximum development. In the air the thickness of the cuticle appears to vary directly with the transpiration, it being thinner on under than on upper leaf surfaces, thinner in stomatal pits than at the surface (figs. 104, 113), and thinner in protected than in exposed situations, as in the basal leaves of *Tilia* in moist woods, in comparison with its top leaves on a dry hill (see figs. 75, 76). As in the case of palisade cells, cutin formation approaches its maximum, both where transpiration is large in amount, as in most xerophytes or even in exposed hydrophytes like the bulrush, and where there is a high ratio of transpiration to absorption, as in alpine and arctic habitats, in peat bogs, and in tropical salt marshes. Cutin formation is increased when ordinary mesophytes (such as wheat) are grown in concentrated solutions, and in the mangrove, cutinization is most marked in the saltiest soils.

In at least one submersed marine plant, *Cymodocea*, the epidermis is cutinized, and the nearly related *Zostera* has no epidermal chlorophyll; it is possible that these features of air leaves are due to the high concentration of the sea water. It should be noted that the cuticle is not always a plastic structure; in the conifers it seems as rigid and as unrelated to environment as are any of the internal tissues.

The rôle of cutin. — Cutin retards the egress of water from leaves, not so much because of its thickness, as because its fatty character

makes it relatively impermeable to water. The transpiration from a peeled apple for a period of three hours is twenty times that from an apple with cuticle intact. A water leaf, exposed to dry air, withers almost immediately because of its uncutinized epidermis. If the stomatal surface of a *Ficus* leaf is coated with wax, the loss of water is enormously reduced, and may amount in one day to but one two-hundredth of that from a water surface of equal area. The cuticle, therefore, is a transpiration-reducing structure of high efficiency, and were it not for the stomata, which entail abundant evaporation, leaves would be almost perfectly protected by their cutin layer. Its value is apparent, not only in dry habitats, but also in peat bogs and in salt marshes, as well as in alpine and arctic conditions, because of inadequate absorption.

The stiffness of most evergreen leaves is due to the cuticle, which thus is of mechanical value, giving protection from winds and storms and also from fungi, insects, and grazing animals (fig. 115). Doubtless the thick epidermis of such leaves as those of *Nerium* and *Ficus* is of mechanical value in addition to its importance in checking evaporation; in the bromelias there is a thin outer layer of cutinized epidermal cells that checks transpiration and a thick but non-cutinized inner layer, whose rôle is chiefly mechanical. In some leaves stiffness is increased further by bast fibers, collenchyma cells, and sclereids (p. 153). The advantage of heavy cutinization to mesophytes (as *Taxus*, *Tsuga*, and *Ficus*) is more difficult to discern. Possibly such plants have limited root systems and relatively slight absorption or imperfect conduction (as in some conifers), the cuticle thus being advantageous in reducing transpiration. Possibly the cutin has no rôle of importance in such plants, representing a surviving structure once of use in some former xerophytic habitat, or, perhaps, a structure which was never of particular advantage.

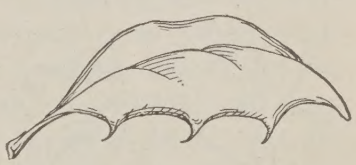


FIG. 115. — A leaf of a broad-leaved sclerophyll, the American holly (*Ilex opaca*), constituting a representative coriaceous leaf of xerophytic aspect, its stiffness being due largely to cutin.

Surface peculiarities; wax and resin deposits. — Many leaves, especially those that appear " glaucous," have a bluish gray surface film of wax, sometimes known as *bloom*, which is readily removed by rubbing (fig. 116). Sometimes these wax deposits are thick, forming a brittle crust, as in *Sempervivum* and in the wax palms, or layers of vertical

rods, as in the sugar cane. *Wax coats* are best developed in xerophytes (*e.g. Agave*, Crassulaceae), and like cutin, they appear to be increased by excessive transpiration. In common with other xeromorphic features, glaucous leaves are abundant in peat bogs and in maritime situations; in solutions of increasing concentration the layer of bloom increases in thickness. Thin as they are, wax coats effectively impede transpiration, the mere rubbing of a glaucous leaf sometimes inducing an increase of a third in the transpired water. Wax coats also retard the heating of leaves. As with hairs, but not with cutin, wax coats are best developed on the under leaf surface, where the stomata are the more abundant. The leaves of many desert xerophytes (as in the creosote bush) are coated with resin, and often have a varnished aspect, shining in the sunlight. Many tropical forest leaves also are shiny. The factors influencing the formation of *resin coats* are unknown. Like wax coats, they may retard transpiration, and it has been suggested that they reflect light, an excess of which may injure the chlorophyll.

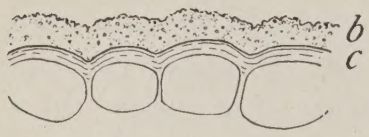
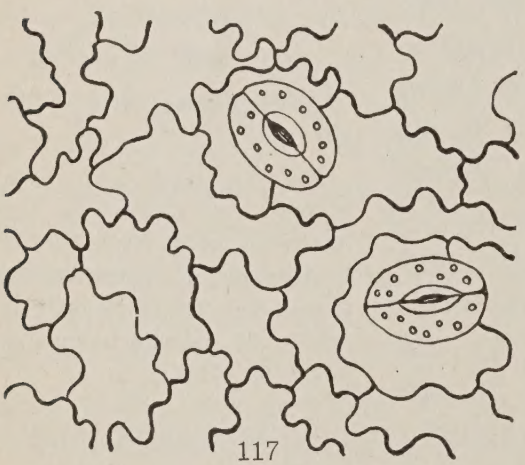
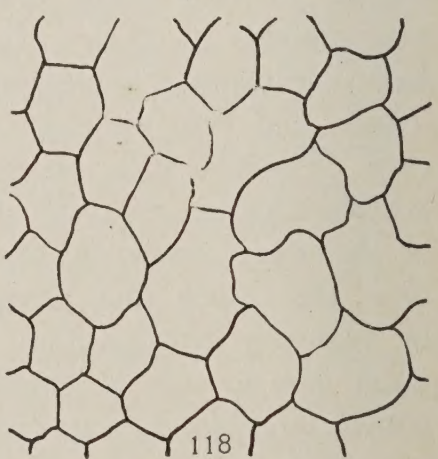


FIG. 116. — A cross section through the leaf epidermis of a xerophytic individual of the glaucous willow (*Salix glaucophylla*), showing just outside the cuticle (*c*) a thick layer of wax grains (*b*), constituting a glaucous bloom; highly magnified.

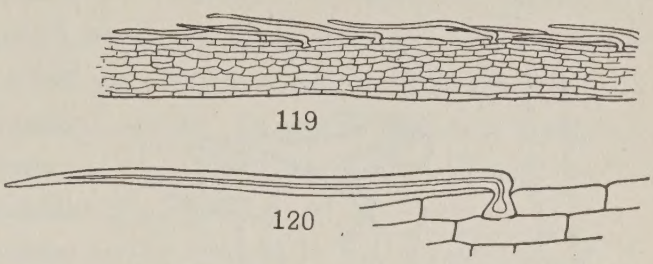




FIGS. 117, 118. — Surface views of the surface of a leaf of Coleus; 117 under epidermis showing the wavy lateral walls characteristic of mesophytic dicotyl leaves; 118, upper epidermis showing the nearly straight lateral walls characteristic of the upper epidermis of mesophytic dicotyl leaves.

It has been shown that shiny leaves become more slowly heated in the sunlight than do similar leaves that are not shiny, so that evaporation probably is reduced thereby.

Floating leaves (as in the water lilies) often have waxy or resinous surfaces, which are highly advantageous in that they prevent the wetting of the stoma-bearing surface, thus facilitating gas exchanges. Many mesophytic leaves also (as in the meadow rue) are not readily wetted, their silvery aspect when thrust into the water being due to an air film next to the waxy surface. Probably few stomatal surfaces are readily wetted, contrasting thus with the surfaces of submersed leaves and with the stoma-free upper surface of many tropical leaves.



FIGS. 119, 120. — Appressed unicellular epidermal hairs from a scale leaf of the winter bud of the Norway maple (*Acer platanoides*): 119, a general view, as seen in lontigudinal section; note the common orientation of the hairs, which is responsible for the silky aspect of the scale leaf; considerably magnified; 120, a single hair; highly magnified.

The lateral walls. — In mesophytic dicotyls the lateral epidermal walls commonly are straight on the upper leaf surface and irregularly wavy on the lower or stoma-bearing surface (figs. 117, 118). In xerophytic and hydrophytic dicotyls and generally in monocotyls, the side walls of the epidermis usually are straight on both leaf surfaces (fig. 97), though in *Maranta* and in various grasses there are wavy walls of striking regularity. In plastic species, waviness culminates in mesophytic conditions; increased and decreased transpiration each result in relatively straight lateral walls. Whether wavy walls have a rôle of importance is not known, though they have been thought to add to the strength of the epidermis and also to give a greater diffusion surface for substances passing from cell to cell.

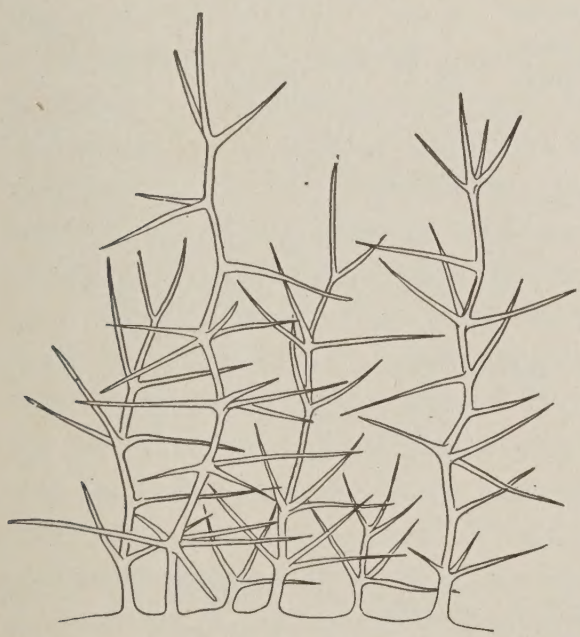
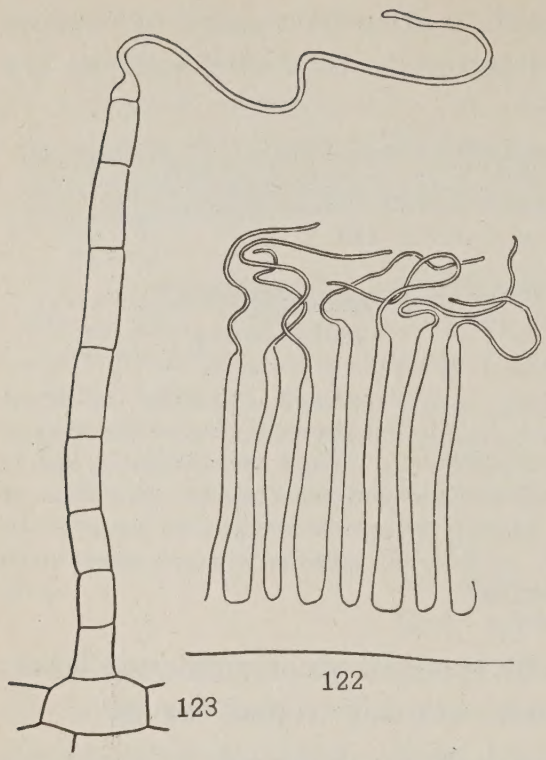


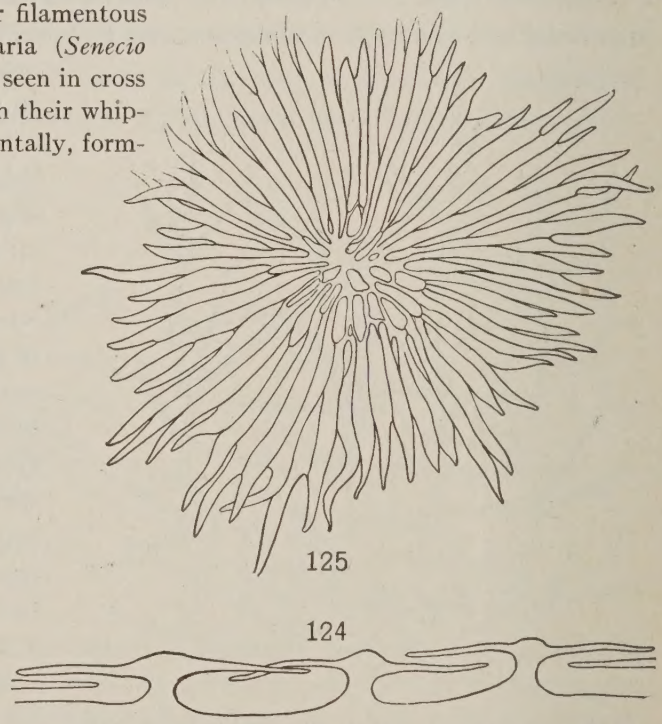
FIG. 121. — Branched multicellular hairs from a leaf of the mullein (*Verbascum thapsus*); considerably magnified.

Structural features of epidermal hairs. — *"Protective" hairs* commonly are stiff, thick-walled structures, which often are dead and air-containing at maturity. They



FIGS. 122, 123. — Multicellular filamentous hairs from a leaf of the cineraria (*Senecio cruentus*): 122, a general view, as seen in cross section, showing several hairs with their whip-like ends, which spread out horizontally, forming chambers between the basal portions of the hairs; note the great length of the hairs in proportion to the leaf diameter; considerably magnified; 123, a single hair; highly magnified.

may be attenuated unicellular structures perpendicular to the leaf surface (as in *Verbena* or in *Potentilla*, fig. 220); more rarely they are parallel to the leaf surface and closely appressed, their common orientation giving the leaf a *silky* aspect (as in *Aster sericeus* and in the bud scales of *Acer platanoides*, figs. 119, 120). Other hairs are similar but multicellular, occasionally being branched (as in the mullein, fig. 121). A *woolly felt*, made up of a dense tangle of long hairs more or less parallel to the surface, extends in various directions (as in the everlastings and cinerarias, figs. 122, 123). *Stellate hairs* divide at the base into horizontal branches, as in various crucifers and mallows (fig. 74). In *Shepherdia* and in *Elaeagnus* the leaf hairs take the form of brown or silvery-gray *scales* (figs. 124, 125). In



FIGS. 124, 125. — Multicellular shield-shaped scale hairs from the leaf of *Elaeagnus:* 124, a general view as seen in cross section, showing the hairs, each of which consists of a vertical stalk surmounted by a horizontal scale; considerably magnified; 125, the terminal scale, as seen from above; highly magnified.

scabrous leaves the surface is papillate or warty, as in many composites.

Variations in hair distribution. — " Protective " epidermal hairs are most abundant in xerophytes, especially in sandy and rocky regions and in deserts, where they often give a characteristic grayish aspect to the vegetation, as in sage-brush deserts. In alpine and arctic regions and in bogs and salt marshes, hairs are less abundant though by no means absent (as in the everlastings, *Ledum*, etc.). Leaves frequently are hairier when young than when mature, many of the hairs soon breaking at a more or less definite weak spot. While some leaves are equally hairy on both surfaces, many leaves are hairy mainly or only on the under (stoma-bearing) surface (as in the silver poplar, fig. 126). In many leaves there is no obvious relation between habitat and hair production, mesophytes frequently and hydrophytes rarely (as in *Pistia* and *Salvinia*) being conspicuously hairy (fig. 203).

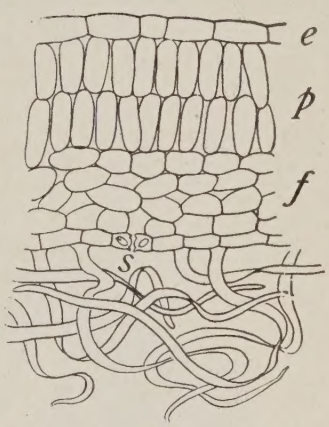


FIG. 126. — A cross section through a leaf of the silver poplar (*Populus alba*), showing a tangled felt of woolly hairs on the under and stoma-bearing surface, the upper epidermis (*e*) being smooth; note that the stoma (*s*) has a well-defined inner ridge, the inner vestibule thus being clearly marked off from the stomatal cavity; this leaf has a representative mesophytic chlorenchyma with two rows of palisade cells (*p*) and a loose sponge tissue (*f*); considerably magnified.

The influence of external factors upon the production and form of epidermal hairs. — Perhaps the most striking variations in hairiness within the same species are found in amphibious plants, such as *Polygonum amphibium*. Aquatic individuals of the latter have smooth leaves (fig. 127), while land forms have leaves covered with numerous stiff and long hairs (fig. 128). Indeed, so different are the two forms of *Polygonum amphibium*, that the hairy form has been regarded as a different species, *P. hartwrightii*, although it is possible to find both forms on the same plant at the edge of a pond. In a number of land species with mesophytic and xerophytic forms, the latter are the more hairy, and in some plants (as *Artemisia canadensis*) winter leaves are more hairy than are the summer leaves. Certain species (as *Convolvulus sepium*) are much more hairy in maritime than in inland situations. From analogy with the excretion of wax and the formation of cutin and of palisade cells, hair formation would appear

to be facilitated by increased transpiration, yet it is difficult to see in just what way the loss of water can produce a complex new structure like the hair of *Polygonum*. Possibly water is a factor which inhibits

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FIGS. 127, 128. — Variation in *Polygonum amphibium:* 127, a branch from the aquatic form with floating leaves borne on a submersed stem; note the lax horizontal stem, the smooth leaves, and the inconspicuous stipules (*o*); this represents the "typical" *P. amphibium;* 128, a branch from the land form (often erroneously called *P. hartwrightii*); note the stout, erect emersed stem, the stiff hairy leaves, and the prominent sheathing stipules (*o*).

hair development, transpiration acting rather as a releasing stimulus (see p. 470).

Some remarkable cases of hair production occur on insect galls. The leaves of *Vitis aestivalis* when young and of *V. labrusca* throughout life are covered with a

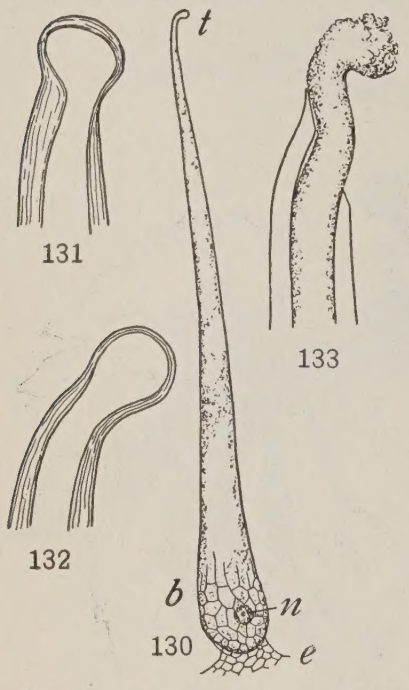
tawny tomentum, while the leaves of *V. vulpina* and *V. cordifolia* are smooth. However, insect galls occurring on the latter species are covered with a hairy coat like that of ordinary leaves in the former species (fig. 129). It would appear that the smooth-leaved species are potentially hairy, needing only the insect stimulus to induce hair production. Similarly, stellate hairs, resembling those usually found on hairy-leaved oaks, may be produced on smooth-leaved oaks through insect activity; in like manner, thorns may be produced on the otherwise smooth leaves of the rose (see figs. 401–403 and adjoining text). It is conceivable that the influence of gall insects upon hair production is essentially comparable to that of xerophytic factors, especially if the insects introduce osmotically active substances into the plant (see p. 300).

FIG. 129. — A portion of a branch of the river grape (*Vitis vulpina*), illustrating the structural transformation that a plant may undergo when attacked by a gall-forming insect: the attack of a gall-fly (*Cecidomyia vitis-pomum*) induces the development of entirely new organs, and parts that otherwise are smooth become woolly-pubescent.

Whatever may be the influence of desiccation or of insect activity upon hair production, neither these nor other external influences appear to modify hair form to any great extent. In most species the shape and structure of the hairs seem inherent, external factors determining only their presence or their absence. In many instances, even the production of hairs seems unrelated to external factors, as possibly in *Coreopsis lanceolata*, where both hairy and smooth forms grow in similar habitats. Perhaps the reference of structures to inherent causes is but an expression of ignorance that may be eliminated upon adequate experimentation.

The rôle of epidermal hairs. — Hairs commonly are believed to have an important rôle in the reduction of transpiration, but the evidence for this view is not abundant. Probably they are much inferior in this respect to cutin or even to wax coats. The most efficient form of hair protection would seem to be that afforded by a woolly felt; it has been shown that the removal of such a felt in *Stachys lanata* results in an increase of twenty to fifty per cent in the transpiration. Evaporating

surfaces artificially coated with hairy felts have been shown to lose much less water than without the hair covering. Similar results may be looked for in scale-covered leaves or in leaves with appressed or branched hairs, where the hairy coat is dense enough to retard the escaping water vapor. In the cinerarias the hairs at first grow erect and then horizontally, producing a chambered layer, while in *Espeletia* there are two or more such layers; the retarding effect of these layers upon escaping water vapor is not difficult to understand. In most hairy plants, however, the hairs are erect and more or less scattered, so that it is difficult to see how they can appreciably retard escaping water vapor, though their presence may to some extent reduce the evaporating surface. Hairs often are most abundant on those parts that most need protection, as on young leaves and on the stoma-bearing surface of adult leaves.



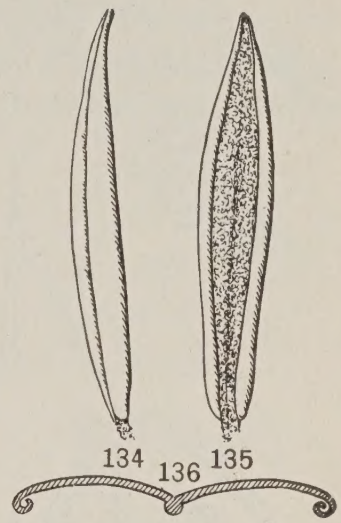
FIGS. 130–133. — Stinging hairs: 130, a stinging hair from the wood-nettle (*Laportea canadensis*), a unicellular structure seated on a slight leaf emergence (*e*); note the bulb-like base (*b*) containing the prominent nucleus (*n*); note also the curved tip (*t*); considerably magnified; 131, 132, the tips of similar hairs, showing the thin neck where oblique breakage occurs; highly magnified; 133, the tip of a broken stinging hair of *Urtica dioica*, showing the poisonous contents flowing out; highly magnified. — 133 from HABERLANDT.

Hairs have been supposed to protect leaves against the injurious effects of heat, light, and cold. In particular, hairy coats on the upper surface have been thought to screen off injurious light and heat rays, it having been shown that hair-clad leaves become heated more slowly than do smooth leaves. The hairs of aquatics (as in *Salvinia*) are of undoubted service in preventing leaf wetting, thereby facilitating unimpeded gas exchange. Stiff hairs, as in mullein, and spiny hairs, as in the thistles, probably afford some protection against grazing animals; in pastures, thistles frequently are untouched, while other plants are eaten greedily.

It must be admitted that the known uses of leaf hairs are small in comparison with their abundant development. While the discovery of advantages now unknown is possible, it is much more likely that most such hairs are of little or no

advantage. The idea should be abandoned that plants have the power to discard organs that are not of use.

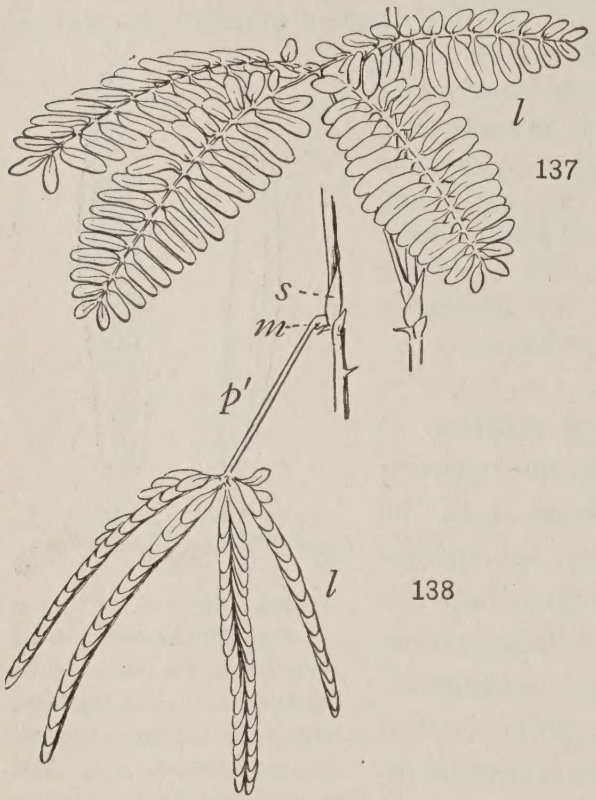
Stinging hairs. — *Stinging hairs* are found in various members of the nettle and spurge families, and consist commonly of a large elongated cell inserted in a cup-shaped emergence (fig. 130). The cell walls are thick and brittle, being silicified or calcified, and the enlarged end is turned slightly to one side (figs. 131, 132). When struck sharply, the hair ruptures obliquely just below the head, leaving a sharp point that suggests a hypodermic needle. The cell contents, which are in a state of high turgor, rush out, injecting an albuminoid poison into the wound, if one is made by the broken hair (fig. 133). Nowhere in plants is there an organ more clearly fitted for a definite function than are stinging hairs, yet there is no evidence that they are of any special advantage to the plants possessing them. Nothing is known concerning the factors underlying their development, since they neither vary appreciably nor grade obviously into other sorts of hairs.



FIGS. 134–136. — Leaves of certain Ericaceae, showing xerophytic features; such leaves are stiff and leathery, largely by reason of prominent cutinization: 134, a leaf of the Labrador tea (*Ledum groenlandicum*), viewed from above; 135, a leaf of the same plant, viewed from beneath, showing a copious woolly tomentum and revolute edges; 136, a diagrammatic cross section of a revolute leaf, that of the bog rosemary (*Andromeda glaucophylla*).

The reduction of transpiring surface. — The most fundamental distinction between xerophytic and mesophytic leaves is in the proportion of surface to volume, the former leaves being narrower and thicker than the latter, and thus presenting a smaller transpiring surface (figs. 173, 174); furthermore, small leaves are much less rapidly heated than are large leaves with equal exposure to the sun. The extremes of divergence in this respect are represented, on the one hand, by hydrophytic or mesophytic leaves one to three cells thick (as in mosses, filmy ferns, and pondweeds, fig. 64), and, on the other hand, by xerophytic leaves that are round in cross section (figs. 232, 233). Within the same species (as *Lactuca scariola*) the xerophytic form has narrower and thicker leaves than has the mesophytic form. In some xerophytes (notably in the Ericaceae) the leaves are *revolute* (*i.e.* with edges curved under), a habit that results in a reduced transpiring surface without a change in volume (figs. 134–136). Frequently sun leaves are concave as viewed from above, hence presenting a reduced surface to the sun, and contrasting with the flatness of shade leaves. The internal transpiring surface of a xerophytic leaf is de-

creased by the reduction of air spaces and by the consequent compact arrangement of the mesophyll; this feature, like the changes in proportion between surface and volume, can be induced experimentally (figs. 69, 70). The most pronounced reductions in the transpiring surface are found in cushion plants and in plants wholly without leaves; these and similar cases will be treated under stems (p. 739).



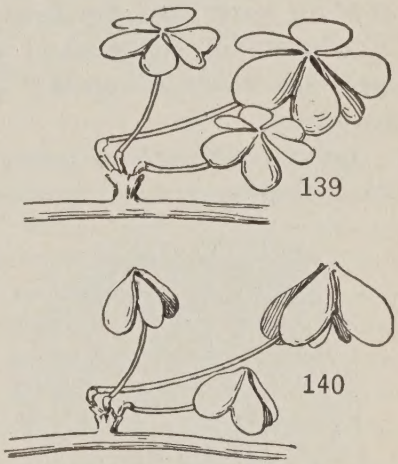
FIGS. 137, 138. — Leaf motility in the sensitive plant (*Mimosa pudica*): 137, an open leaf; 138, a leaf whose leaflets (*l*) have been closed by mechani cal impact; note also that the petiole (*p*) has dropped; *s*, stipule; *m*, pulvinus.

Reduction in transpiration due to leaf orientation. — Diaphototropic leaves appear to be placed in a position favorable for maximum synthesis, while the vertical or profile position seems to make possible a reduction in transpiration, by reason of less direct exposure to the sun. The leaf orientation of *Lactuca* (fig. 88) and of *Nicotiana* (fig. 89) may be regarded as advantageous from the standpoint of protection from transpiration, the latter plant exhibiting, as the transpiration increases, a series of leaf positions varying from horizontal to vertical.

Motile leaves. — *The phenomena of leaf motility.* — In many Leguminosae (as in the clovers and locusts) and in *Oxalis* the leaflets of the compound leaves close by night (especially in cool weather) and open by day; such closing movements have been called *photeolic movements* or, less correctly, sleep movements or nyctitropic movements. In many legumes desiccation causes the leaflets to assume the closed position; in *Mimosa* contact also produces the same effect (figs. 137, 138), and in *Desmodium gyrans* there are movements apparently without external cause. While most motile leaves are compound (figs. 139, 140), some simple leaves exhibit motility, as in *Portulaca*

oleracea and in *Euphorbia polygonifolia*, those of the latter closing along the median line like a book.

Most leaf movements are due to changes in the turgescence of the delicate cells that make up the body of the enlarged base (known as the *pulvinus*) of the petiole or petiolule (leaflet stalk); the central position of the delicate conductive bundle and the absence of mechanical cells facilitate motility. Closing may be due to a decrease of turgescence, as in drought, or to an increase, which is greater on one side than on the other, as in the night closing of the bean leaflets. The rapid closing of *Mimosa* by contact is due to the sudden escape of water from the cells into the adjoining air spaces, while subsequent opening is due to its slow reëntrance; the slower photeolic movements are made possible by a change in the permeability of the cell membranes occasioned by a change in illumination. The leaflets of the hydrophyte, *Marsilea*, close if emersed, but not if floating, possibly because water contact preserves the necessary turgescence, or possibly because water may mechanically inhibit closing.



FIGS. 139, 140. — Leaf motility in *Oxalis:* 139, open leaves as seen by day; 140, closed leaves as seen by night.

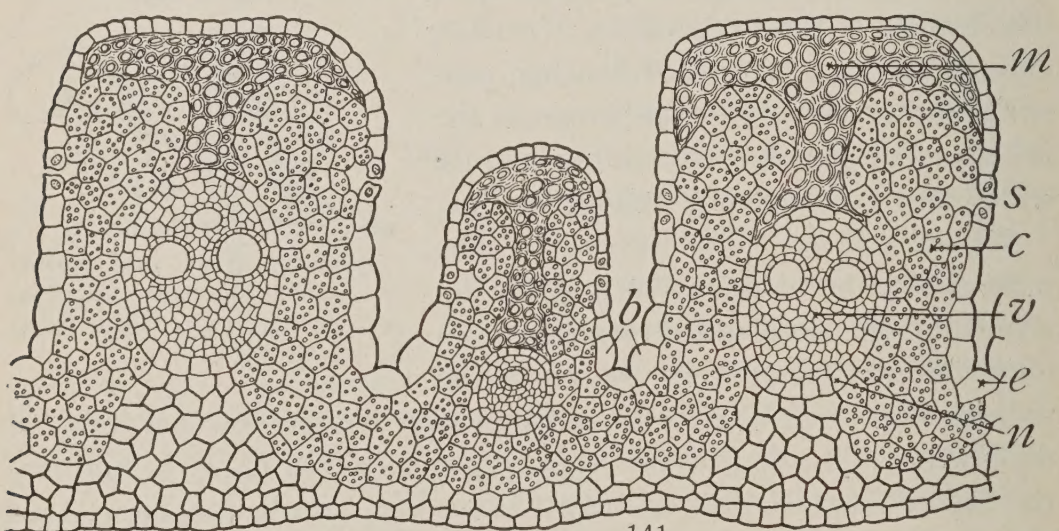
The advantages of leaf motility. — The most obvious advantage which plants derive from leaf motility is protection from excessive transpiration, by reason of the reduced surface in the closed position that is assumed as a result of desiccation. In some leaves (as in those which fold along the midribs) the exposed surface may be reduced one half, and it may be reduced almost as much in a plant like *Mimosa*, where the leaflet segments closely overlap one another. In other cases, closing means rather a changed orientation, as in the drooping leaflets of the bean, or in the erect leaflets of the beach pea, which assume a temporary profile position, suggesting the permanent profile position of *Lactuca* and *Silphium*.

Night closing is a much more common phenomenon than is drought closing, but its advantage is not obvious. Protection from cold has been suggested, but this view has no supporting evidence; motile leaves often are open on cool days and closed on warm nights. The facilitation of nocturnal transpiration also has been suggested, it

being supposed that verticality prevents wetting by dew; but there is no apparent advantage from increased nocturnal transpiration. Perhaps nocturnal closing is quite useless, as is pretty certainly the case with such extraordinary movements as those of *Desmodium gyrans* and the contact movements of *Mimosa*.

Leaves are subject to passive movements through the action of wind or water. The leaves of the reed (*Phragmites*) are attached to the stem in such a manner as to swing around in the wind like a weather vane, their ready yielding preventing injury. Compound leaves, as in the coconut and in many submersed aquatics (as the water milfoil), offer but little resistance to wind or water currents, and hence escape injury, while large, simple leaves, as those of the banana (fig. 152) or of the water lilies, are shredded when similarly exposed. The lateral flattening of the petiole of the aspen and of other species of *Populus* results, even in the lightest breezes, in an almost constant trembling of the leaf, a phenomenon without obvious advantage.

Infolded and withered leaves. — Many grass leaves (known as *involute*) roll inward when exposed to desiccation, owing to the loss of water from large, turgescent



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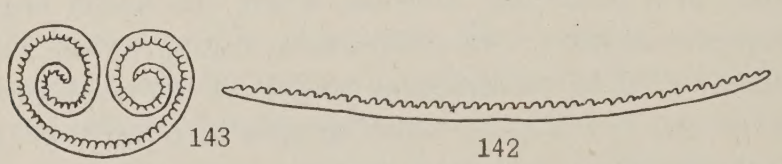

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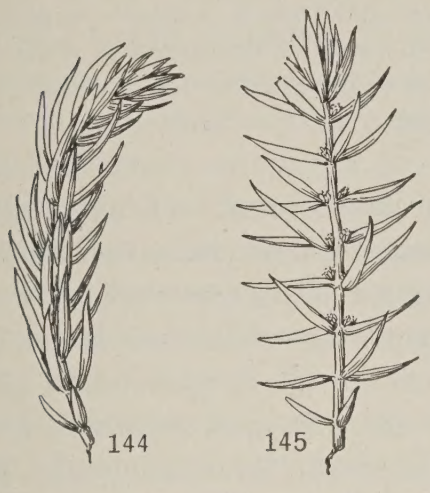
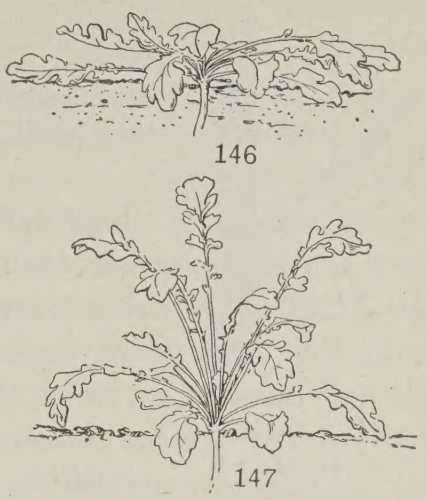
FIGS. 141–143. — Cross sections of the involute leaf of a xerophytic grass, the sea sand reed (*Ammophila arenaria*): 141, a cross section (highly magnified), showing chlorenchyma (*c*) composed of cells that differ from palisades in form and from sponge cells in compactness; the stomata (*s*) are confined to the upper (here the more protected) epidermis (*e*); note in the sinuses large water-containing cells (*b*), whose changes in water content account largely for leaf closing and opening; *v*, conductive tracts; *n*, bundle sheath; *m*, mechanical tissue; 142, a diagrammatic cross section of a turgid open leaf; 143, a diagrammatic cross section of a desiccated inrolled leaf; 142 and 143 slightly magnified.

thin-walled cells, which are arranged in longitudinal rows, and often are below the level of the other epidermal cells (figs. 141–143; also fig. 163). The surface ex-



FIGS. 144, 145. — Shoots of the juniper (*Juniperus communis*), showing varying leaf orientation: 144, a shoot as seen in winter; note the ascending or erect leaves, whose orientation probably is due to a preponderance of growth beneath (hyponasty); 145, a shoot as seen in summer; note the spreading leaves, whose orientation probably is due to a preponderance of growth above (epinasty).



FIGS. 146, 147. — Rosettes of the peppergrass (*Lepidium*), showing varying leaf orienta ion: 146, a winter rosette with leaves closely appressed to the ground through a preponderance of epinastic growth; 147, the same rosette, after a stay of several days in a greenhouse; most of the leaves have an erect or ascending orientation by reason of a preponderance of hyponastic growth.

posure of a grass leaf may, by such a process, be decreased to a fraction of its original area, doubtless resulting in a much-reduced transpiration, particularly because the stomata are on the infolded surface. Often the leaf ridges meet, making closed chambers of the furrows. The wilting of leaves, also due to reduced turgescence involves some reduction of transpiring surface and also the complete closure of stomata, greatly reducing water loss. The water loss from turgid sunflower plants has been found to range from 5 to 10 times as much as from wilted ones. Various mosses (as *Orthotrichum*), the rose of Jericho (*Anastatica*), and some ferns (as *Selaginella lepidophylla* and *Polypodium polypodioides*) curl up when desiccated, exposing a reduced transpiring surface; their sudden uncurling when moistened has given rise to the term *resurrection plant*. Such movements as those exhibited by the leaves of *Polytrichum*, due to changing water content (figs. 207, 208), are of significance in relation to transpiration, since the closely appressed leaves of desiccated individuals have a greatly reduced aggregate surface.

Epinasty and hyponasty. — If a leaf exhibits curvatures by reason of greater growth at the upper surface, it is said to display *epinasty*, while if the greater growth is at the lower surface, it displays *hyponasty*. Various plants, as *Juniperus* (fig. 144) and *Sempervivum*, manifest hyponasty in the autumn, the erected leaves becoming closely appressed to the stem or to one another, while epinasty the following spring results in leaf horizontality and increased surface exposure (fig. 145). In other cases, especially in rosette plants (as *Lepidium*), the reverse is

seen, the winter leaves being horizontal and closely appressed to the ground as a result of epinasty (fig. 146), while spring hyponasty results in their erection (fig. 147). In all cases the autumn reaction results in a reduced surface exposure, and hence is favorable to protection from cold and from excessive transpiration, while the spring reaction results in an increased surface exposure, and hence facilitates synthesis.

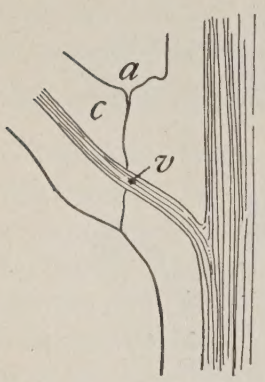


FIG. 148. — A diagrammatic vertical section through the basal region of a mature leaf of the cottonwood (*Populus deltoides*), showing the initial stages of leaf fall; the absciss layer develops along the plane, *a*; the cortical tissues (*c*) separate first, and the leaf falls when the vascular region (*v*) is ruptured; somewhat magnified.

Leaf fall. — *The absciss layer.* — Leaves differ greatly as to duration, most cotyledons and many delicate leaves living for only a few weeks or even days, while evergreens may retain their leaves for a year or two, or even for ten or more years, as in the pines and the cycads. In most deciduous trees and shrubs the leaves remain for some months, the exact period varying widely, as the season is long or short. *Leaf fall*, especially in deciduous trees and shrubs, is brought about by the development of a special layer of separation or *absciss layer* at the base of the petiole, representing the final phase of leaf activity. The cells of this layer differ from the adjoining cells in their greater turgescence and in possessing denser cytoplasm and more abundant starch, and in the relative thinness and slight lignification of their walls. Soon the walls become mucilaginous and the cells then disintegrate along the plane of separation (fig. 148); the rupture of the conductive tract by wind or otherwise completes the process, the leaf falling to the ground. At leaf fall, and sometimes before, the wound is healed by the development of a protective cork layer; thereafter, the place of leaf attachment is marked by a *leaf scar*, whose shape and structure vary with the species (figs. 364–366). In some compound leaves (as in the hop tree and the Virginia creeper) absciss layers may develop first at the base of the leaflets, leaving the stems with a number of bare petioles. Sometimes the absciss layer is imperfectly if at all developed, so that the dead leaves remain on the tree, as in the beech and in various oaks. In most herbs there is no definite absciss layer, the leaves remaining attached until after death.

Deciduous and evergreen trees. — *Deciduous* trees, as commonly understood, shed all their leaves at once, at the beginning of an un-

favorable season, while *evergreens* shed their leaves from time to time, or, if all at once, only after the new leaves have developed (fig. 149). While the distinction between evergreen and deciduous trees is well marked in cold temperate climates, such is not the case in the tropics, where the same species or even the same individual may be evergreen one year and deciduous the next, or evergreen in low grounds and deciduous elsewhere; or the tree top may be deciduous and the basal limbs evergreen. Deciduous trees (figs. 150, 151) scarcely need subdivision (except that some tropical forms may have two or more periods of leaf shedding and renewal each year), but evergreens may be subdivided into (1) the tender-leaved evergreens of the rainy tropics, such as tree ferns and bananas (fig. 152); (2) evergreens with broad and stiff leaves, the so-called broad *sclerophylls*, as the live oak and the holly (fig. 115); (3) evergreens with stiff, needle-like leaves, as in the pine and the spruce (fig. 263); (4) succulent desert evergreens, as *Agave*

FIG. 149. — A winter landscape, showing contrast between deciduous and evergreen trees; the evergreens are white pine (*Pinus strobus*) and the deciduous trees are mostly elms (*Ulmus americana*); the pines are excurrent while the elms are deliquescent; Lakeside, Mich. Photograph by FULLER.

(fig. 227); and (5) leafless evergreens, such as the cacti (fig. 342) and *Ephedra*. A transition to deciduous trees is seen in the potential

evergreens, such as *Ilex decidua*, which, though deciduous in the northern states (as suggested by the specific name), is evergreen farther south, as are various oaks that are deciduous in the north. *Magnolia grandiflora*, a true evergreen in the Gulf states, retains its leaves at its northern limit, although they die before the winter is over, thus resembling the beech and those oaks in which the autumnal absciss layer is imperfectly developed.

The causes of leaf fall. — The leaf behavior of deciduous trees and of tropical evergreens obviously is related to external factors, in the

FIG. 150. — A sugar maple (*Acer saccharum*) that has grown in the open and thus is symmetrical, the general shape being conical with a rounded apex; this figure represents a deciduous tree in summer condition; Lancaster, Ohio. — Photograph by HYDE.

FIG. 151. — The same tree shown in fig. 150, but in winter condition; note that the conical shape is due to the gradual change in branch direction from horizontal or descending at the base to ascending and finally to vertical at the apex. — Photograph by HYDE.

former being associated with climatic periodicity (either of moisture, as in the monsoon forests of India, or of temperature, as in the northern deciduous forests), while in the latter it is associated with uniform moisture and temperature. That the deciduous and the evergreen habits are related to external conditions may be inferred from many trees and shrubs (*e.g.* poison ivy, Virginia creeper, various oaks) which shed their leaves in regions of cold winters, but retain them in warmer climates; furthermore, various plants (as the grape and the peach) become evergreen in uniform tropical climates, and even those species

that remain deciduous (as the persimmon and the mulberry) have much longer periods of leafage.

The exact factors involved in leaf fall, that is, in the development of the absciss layer, are imperfectly known. In the monsoon forest and in other regions of periodic drought, it is probable that leaf fall results directly from the desiccation incident to the increased transpiration and decreased absorption during the dry period. Autumnal leaf fall in cool climates probably is due to desiccation resulting from continued transpiration at a time when absorption is diminished by reason of low temperature, although desiccation due to dryness in the soil or air may cause the absciss layer to develop in early summer. A severe frost in early autumn may retard leaf fall through injury to the tissues that develop the absciss layer.

FIG. 152. — A group of banana trees (*Musa*); the gigantic leaves have been much frayed by the wind (marginal mechanical tissue being poorly developed), giving the effect of a pinnate palm leaf; the shrubs beneath the banana trees are coffee plants (*Coffea arabica*); Xalapa, Mexico. — Photograph by LAND.

The cause of the leaf fall in evergreens is as yet scarcely to be conjectured, there being little or no obvious relation to external factors, except when the old leaves are in a sense pushed off by growing shoots. Perhaps leaf activity gradually becomes impaired through the continued accumulation of excreta and the increased clogging of the stomata by dust, or perhaps such leaf fall is governed by internal factors. Investigations on the duration of evergreen leaves show that some trees such as *Arbutus menziesii* retain their leaves for 12 to 14 months only, others such as species of *Pinus*,

Picea, *Abies*, *Tsuga*, and *Pseudotsuga* for 3 to 8 years, or occasionally for 12 years, while the leaves of *Taxus*, the yew, may remain on the tree for as long as 20 years.

The advantages of leaf fall and of the evergreen habit. — The shedding of leaves at the inception of a cool or dry period is of inestimable advantage, especially in trees with delicate leaves, because of the enormously reduced transpiration thus resulting. The leafless tree is one of the most perfectly protected of plant structures, since impervious bud scales and bark cover all exposed portions. So close is the relation between leaf texture and leaf fall that in temperate or in cold climates one almost may determine by the feel of a leaf whether it is deciduous or evergreen. While evergreens are more subject to winter transpiration than are deciduous trees, they have compensatory advantages, such as lower summer transpiration, less danger from frosts in the growing season, and readiness for synthetic activity at all seasons. The broad sclerophylls abound chiefly in regions of winter rain, their advantage seeming to consist in the possibility of utilizing every day suitable for synthesis, while they are also well protected from winter cold and summer drought. The advantage of the delicate evergreen leaf is obvious where uniform moisture and temperature prevail.

Protective features in the cell sap and in the protoplasm. — Many plants appear to be very drought resistant although lacking in such protective structures as have been described. For example, many plants transpire less and some much less in hot weather than at other times, due to partial or complete wilting causing the entire closing of the stomata. The importance of such protective wilting has been much underestimated, for drought resistance often may be defined as ability to recover readily after complete wilting. Such ability seems, for the most part, associated with a high rate of carbohydrate synthesis, intense transpiration, reduced size, and high osmotic pressure. The capacity to endure without injury an intense loss of water is connected with the capacity of the protoplasm to endure considerable fluctuations in its mass without the loss of vital activity and without the appearance of irreversible coagulation. The problem of drought resistance thus falls within the province of colloidal chemistry together with other phenomena such as the power of resistance to frost. Most plant activities take place between 0° C. and 45° C., and at certain temperatures (varying with the species) beyond those at which growth is checked, life itself is destroyed. Death from freezing generally has been attributed to the desiccation of the protoplasm incident to the withdrawal from the cell sap of water which contributes to the formation of ice crystals. Many plants show remarkable resistance to freezing temperatures, and it is probable that such resistance in many instances is due to the presence in the cell of sugars and other soluble carbohydrates. Frost resistance seems also to result from the increase of colloids in the cells. Sugars result in high osmotic pressure in the cell sap and

this high pressure may be habitual, as in many xerophytes, or there may be changes of pressure accompanying temperature changes.

An instance of varying pressure is seen in the numerous northern evergreens, whose leaf cells in winter contain sugar instead of starch, and thus have a more concentrated cell sap than in summer; it is believed also that sugar retards the coagulation of proteins which otherwise would be induced when the cell salts become concentrated. The resistance of red leaves to low temperatures also may be associated with their high sugar content. The injury occasioned in early autumn or in late spring by a frost that in winter would be harmless may be explained in part by the lower sugar content at such seasons. It must be admitted, however, that many cases of resistance to freezing or to desiccation as yet remain unexplained although in both instances resistance seems increased by the increase of colloids within the cell. Perhaps the best illustrations of such unexplained resistance are found among the bacteria, algae, and lichens. Bacteria in the so-called resting stages are able to endure the high temperatures of hot springs or the low temperature of liquid hydrogen, and are able to withstand the desiccation of the desert. Even algae, though characteristic hydrophytes, may occur, apparently unprotected, on dry rocks or in the snow and ice, the blue-green algae in particular being about as resistant as are the bacteria. Lichens absorb and transpire water quickly, enduring long droughts in a desiccated condition without injury; indeed, they may be regarded as among the most resistant of plants, in spite of their lack of obvious protective structures, a fact that is all the more remarkable since they are complexes of algae and fungi, groups which separately flourish best in water and in moist woods respectively. Desiccation in these plants induces merely a resting stage or stage of suspended animation, in which the small amount of water needed to preserve life is retained with great tenacity. Very probably it is the ability of these plants to retain this necessary modicum of water that accounts for their great resistance to detrimental factors. The ultimate cause of resistance here would seem to be some " specific property of the protoplasm," whose nature is as yet unknown.

FIG. 153. — A tree yucca (*Yucca arborescens*); note the rigid, needle-like, many-ranked leaves, which lop back against the stem, serving long after death as a protective covering; among the shrubs is the creosote bush (*Larrea tridentata*); Victor, California. — Photograph by E. W. COWLES.

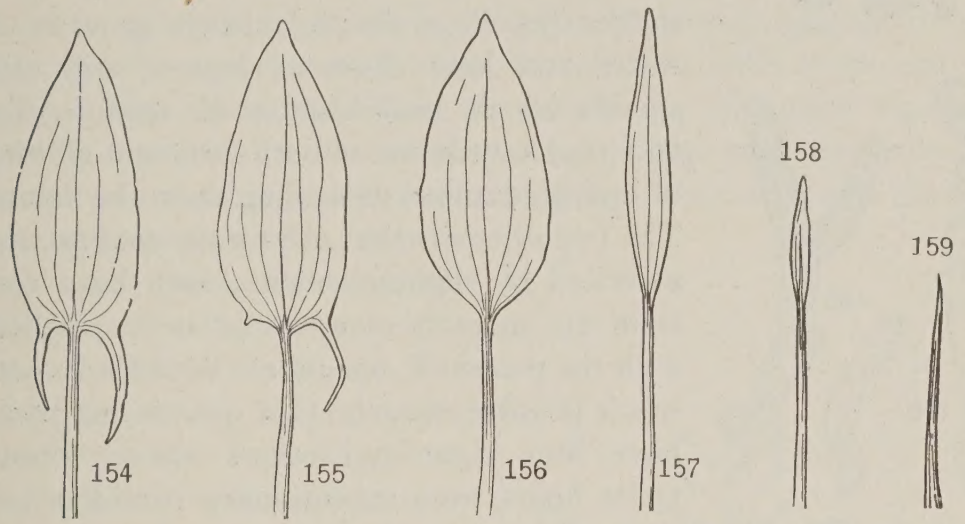
Protection by coverings of snow and of dead leaves. — The mantle of fallen leaves which covers the ground in forests, and the dead leaves remaining on the grasses and other plants of meadows and swamps, are of great value in protecting herbaceous vegetation from the rigors of winter. On some trees, as in *Yucca* (fig. 153) and in various palms (fig. 258), the leaves or leaf bases remain on the stem

after death, forming a thick protective layer. Similarly, in cold climates the snow cover is of great protective value. In alpine meadows the deep and long-enduring mantle of snow most effectively protects the alpine herbage from the severities of winter. Layers of snow or leaves tend to conserve the soil warmth, and thus are of value in protecting the subjacent vegetation from the deleterious effects of sudden temperature changes, but they are of much greater value in reducing transpiration to a minimum at a time when the low soil temperature prevents absorption. The winter killing of unprotected wheat and of other vegetation is in most instances due to excessive transpiration rather than to freezing.

Summary on transpiration and carbohydrate synthesis. — A review of the preceding pages seems to indicate that there often exists a reciprocal relation between the structural requirements associated with transpiration and carbohydrate synthesis. The form of leaf best fitted for maximum synthesis seems least fitted for the reduction of transpiration. Hydrophytes and mesophytes as a class have thin expanded leaves well fitted for synthetic activity because their structure facilitates the reception of light and the absorption of carbon dioxide. Many xerophytes on the other hand have small thick leaves that reduce gas exchanges, thus reducing both transpiration and carbohydrate synthesis. Investigations seem to justify the conclusion that all influences that result in the increased loss of water by the plant or in a restricted water supply to developing leaves lead to essentially similar changes in leaf structure. Many of these structural changes which may be termed *xeromorphic* tend to facilitate the water supply quite as much as to check transpiration. Such changes as the increased development of veins in the leaf tend to increase the water supply, while the increase in the number of stomata and in the amount of palisade development also tends to increase carbohydrate synthesis. In consequence of these changes xeromorphic plants often have high rates of transpiration as well as high rates of carbohydrate synthesis. It would appear, however, that many plant structures are not thus related to environment. The xeromorphism of such leaves as those of the ericads, conifers, and begonias, features that are equally advantageous with those of other xeromorphic leaves in reducing transpiration, appear inflexible when subjected to varying conditions. But as conditions of soil and climate are subject to constant change, those species whose structures become modified accordingly would seem to be best fitted to survive. The extinction of species often may have resulted from a lack of plasticity.

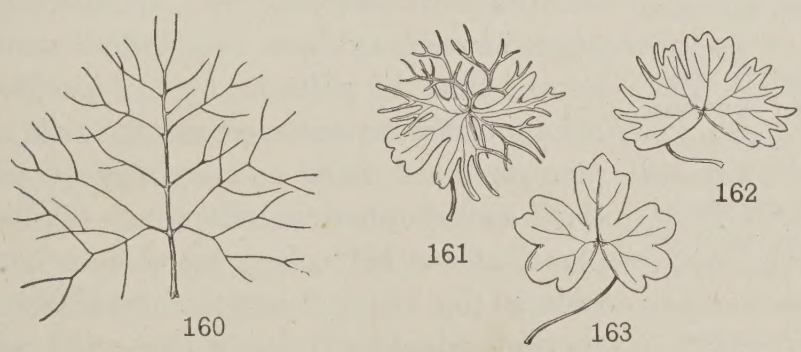
6. VARIATIONS IN LEAF FORM

The significance of leaf variation. — Distinctions between plant species commonly are based upon the forms of leaves and of other organs, hence the determination of the causes underlying form is among the most fundamental of problems. In many species (*e.g. Sagittaria hetero-*



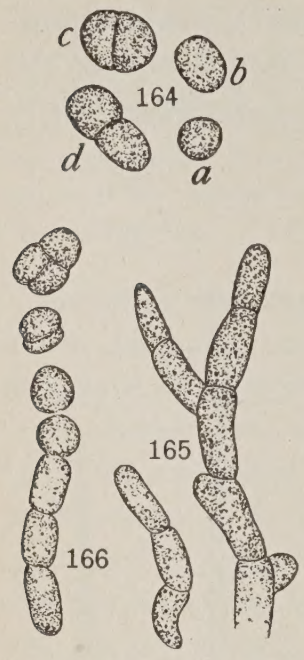
FIGS. 154–159. — Leaf variation in an arrowhead (*Sagittaria heterophylla*): 154, a representative air leaf; 155, 156, air leaves from plants in deeper water than those bearing such a leaf as figured in 154; note the reduction or absence of the basal lobes; 157, 158, leaves from plants in deep water; 159, a submersed bladeless leaf (phyllode); all the variants here figured may be found in a single vegetative colony connected (at least originally) by underground stems; they may be found also on a single individual at different developmental stages, the phyllode appearing first and the broad leaf last.

phylla, figs. 154–159) there is a wide variation in leaf form which is connected definitely with external causes. When comparable differences in leaf form constitute specific characters, it is a tenable hypothesis that the present species are the fixed descendants of once plastic an-



FIGS. 160–163. — Leaf variation in the white water-buttercup (*Ranunculus aquatilis*): 160, a water leaf, entirely submersed during development; 161, 162, leaves transitional between air leaves and water leaves; 163, an air leaf.

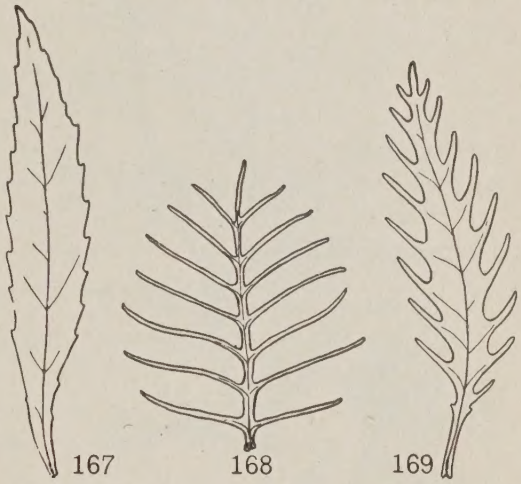
cestors that had a range of variation broad enough to include differences as great as those that to-day characterize distinct species. For example, among the buttercups there are some species (as *Ranunculus septentrionalis*) which always grow on land, and whose leaves are divided but not finely dissected, while other species (as *R. circinatus*) always grow in the water and have dissected leaves; still other species (as *R. multifidus* or *R. aquatilis*, figs. 160–163) have leaves of both sorts and all kinds of intergradations, depending upon the habitat. The hypothesis is that the former species, characterized by slight plasticity, each have come from an ancestry comparable as to plasticity with the present *R. aquatilis*. Another hypothesis is possible, namely, that some forms always have been rigid and others always plastic. Quite apart from evolutionary considerations, the study of the cause of leaf form is important, because of its bearing upon the fundamental problems of plant behavior, and because of its relation to the rôle of leaves, including the advantages and disadvantages associated with the different leaf forms in various habitats.



FIGS. 164–166. — Variation in *Stigeoclonium*: 164, the palmella form, consisting of isolated spherical (*a*) or oblong (*b*) cells; *c*, *d*, vegetative reproduction by means of fission, *c* showing an early stage in which a dividing wall is formed, and *d*, a later stage, just before the two daughter cells separate; 165, the filamentous form, in which the elongated individual cells cohere in simple or branched chains; 166, a filament that has been placed in a concentrated solution and is beginning to break up into the palmella stage; note the rounding of the cells and their subseqent separation; highly magnified. — After LIVINGSTON (drawn from a photographic reproduction).

Form variations in thalloid plants. — The variations in body form exhibited by algae and fungi are in many respects comparable to those of leaves, though somewhat simpler, thus clearly meriting consideration here. In nature the alga, *Stigeoclonium*, exhibits two widely contrasting forms: one, the palmella form, once thought to belong to the separate genus, *Palmella*, is common on moist bark and consists of relatively thick-walled spherical cells, which divide in any plane, and either cohere in colonies or become isolated (fig. 164); the other form is filamentous, the individual cells being elongated and relatively thin-walled, and dividing in but one direction (fig. 165). It has been shown that if the

filamentous form is grown in a medium of relatively high osmotic pressure, the palmella form is produced, the cells soon bulging out and becoming spherical, and later separating; subsequent divisions occur in all planes (fig. 166). On the other hand, the filamentous form is produced, if the palmella cells are grown in a medium of relatively low osmotic pressure. While only young palmella cells can grow into filaments, adult filament cells are capable of developing directly into palmella cells, contrary to the general rule that adult forms are not plastic. The filamentous form appears to be the more vigorous, probably because the low concentration of the medium facilitates absorption and consequently a dilute cell sap, which in turn is thought to favor growth and luxuriance. Long cultivation in a given medium results in "accommodation" to that medium; for example, the cell-sap concentration in a plant grown for a long time in a medium of low concentration is less than that in one similarly grown in a medium of high concentration. Furthermore, a filament grown for a long time in a dilute solution reacts more quickly to a concentrated solution than one that has just been produced from palmella forms of long standing.



FIGS. 167–169. — Leaves of the mermaid weed (*Proserpinaca palustris*); 167, an air leaf; 168, a water leaf; 169, a transitional leaf.

As might be expected, sea water induces the palmella form of *Stigeoclonium;* also if a salt solution of low concentration is allowed to evaporate, the palmella form gradually develops, owing to the slow increase in concentration. The palmella form also may be induced by exposure to transpiration (the condition under which this form probably develops on trees), or to low temperatures, even if the solution is dilute. All changes in form thus far noted may be related to water, the palmella form being produced in conditions where absorption is low (solutions of high concentration or low temperatures) or evaporation high (air cultures), or, in other words, where the cell sap becomes relatively concentrated; the filamentous form, on the other hand, is produced if absorption is high and transpiration lacking, that is, if the

cell sap becomes relatively dilute. The palmella form can be produced also by chemical stimulation, notably by toxic salts (*e.g.* salts of copper, lead, and silver), and by solutions of bog water, where the low concentration excludes osmotic pressure as a causative factor.

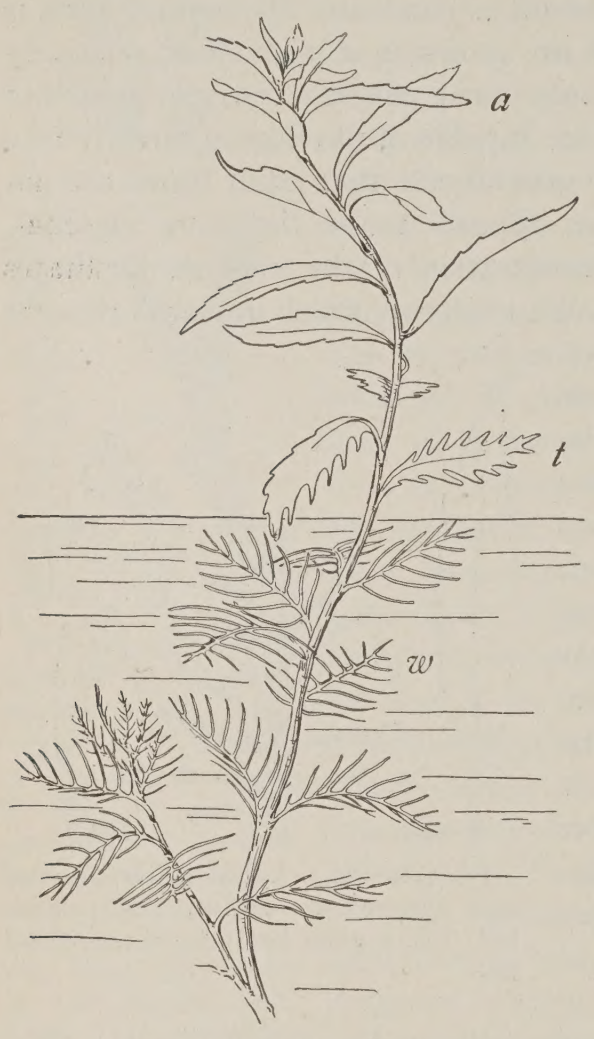
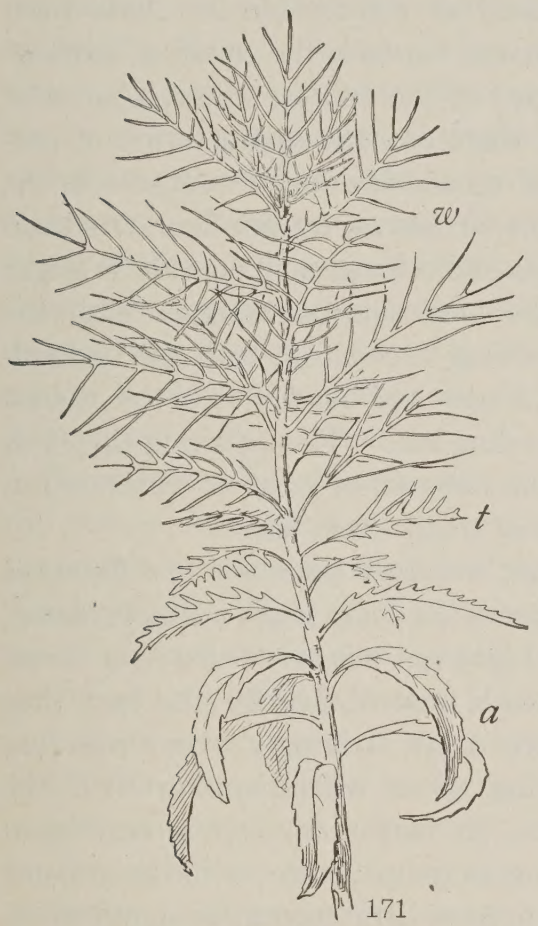
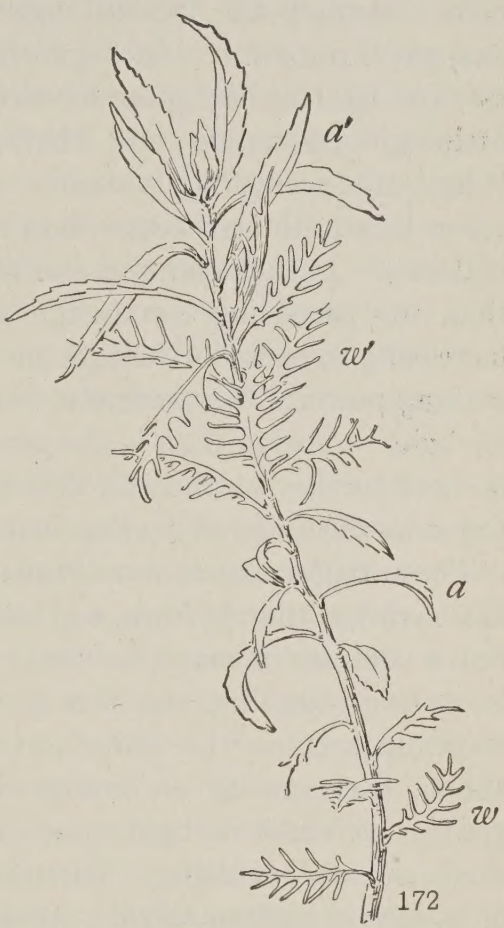


FIG. 170. — Leaf variation as exhibited ordinarily by the mermaid weed (*Proserpinaca palustris*); note the finely dissected water leaves (*w*), the nearly entire air leaves (*a*), and the transitional leaves (*t*) just above the water surface.

Form variations in amphibious plants. — *The phenomena.* — No plants show greater variations in leaf form and structure than do amphibious plants, which may be subject alternately to submergence and to desiccation. For example, the mermaid weed, *Proserpinaca palustris*, has almost entire, lanceolate air leaves, and finely pinnatifid water leaves, larger in outline, though of less weight (figs. 167–169, 170). The variations of *Radicula aquatica*, one of the cresses, are very similar, and even more striking, since the air leaves are quite entire, while the water leaves may be twice or thrice pinnately dissected. In the water parsnip, *Sium cicutaefolium*, the early radical leaves are much dissected, while the later leaves are simply pinnate. In various buttercups there are similar form changes, involving palmate rather than pinnate leaves (figs. 160–163). Another group of amphibious plants, represented by *Alisma*, *Castalia*, and *Potamogeton natans*, have narrow, thin, submersed leaves and broad, thick, aerial, or floating leaves, while in *Sagittaria*, similar differences are supplemented by the development of basal lobes (figs. 154–159).

Not all amphibious plants, even in the above genera, are equally plastic. For example, *Radicula palustris* has pinnately compound leaves in all habitats, and *Sagittaria graminea* and *S. lancifolia* develop air leaves without basal lobes. Few plastic species are equally variable at all times, the early leaves of *Proserpinaca* and *Sium* being much divided, regardless of the habitat, while the latest leaves react much less readily than do the plastic intermediate leaves. After *Sagittaria* has





FIGS. 171, 172. — 171, a shoot of the mermaid weed (*Prosperpinaca pulustris*) that has been placed in water after growing for some time in the air; note the transitional leaves (*t*) between the air leaves (*a*) below and the water leaves (*w*) above; *Proserpinaca* has a phyllotaxy of high rank, there being a number of orthostichies (p. 65); 172, a shoot of the mermaid weed that has been grown successively in water, air, water, and air; note the corresponding sets of leaves, *w*, *a*, *w'*, *a'*. — After McCALLUM.

commenced to produce sagittate air leaves, submergence results commonly in the development of new air leaves with long petioles rather than in a renewed development of water leaves. However, *Limnophila* seems to be about equally plastic at all times, and in *Myriophyllum heterophyllum*, even the emersed flowering branches develop water leaves upon submergence.

The causes of leaf variation in amphibious plants. — If a *Proserpinaca* plant is removed from the water, entire leaves at once begin to develop

instead of dissected leaves; on the other hand, dissected leaves soon appear if an air-grown specimen is placed in water (fig. 171). Alternations of the two leaf forms may be produced by alternating the conditions (fig. 172). Such experiments show the extreme plasticity of the plant, and the close relation existing between leaf form and environment. Among the factors suggested as responsible for these form changes is nutrition. In *Sagittaria* and *Castalia* the smallest, narrowest, and lightest leaves are developed in the deepest water, where but little light penetrates, and where, therefore, the manufacture of carbohydrates necessarily is slight. Even in *Sium* and *Proserpinaca*, the water leaves, though larger than the air leaves, contain less structural material. In such plants as *Castalia* and *Alisma* each new leaf is larger than the preceding, as though the food supply increases with the increasing expanse of foliage, involving a constant increase in food-making power. Furthermore, each new leaf usually is better placed for light reception than is the preceding leaf. The nutrition theory is favored further by the fact that the removal of roots or leaves is followed by the renewed development of small water leaves.

The nutrition theory is inadequate, because it accounts for differences in size rather than in form, and because nutrition is not a simple factor, but a complex of many factors. Light has been regarded as a direct formative stimulus, but this is made improbable by the fact that leaves just below the water surface differ strikingly from those just above, there being no intergrading series corresponding with the gradual decrease in light; besides, air leaves develop as readily in shade as in full sunlight. Variations in temperature, or in the amount of oxygen or carbon dioxide, seem to have little formative significance.

The factor which appears most directly related to leaf form in amphibious plants is transpiration. In *Proserpinaca* the water leaf can be produced in a saturated atmosphere, appearing to show that transpiration results in the formation of air leaves, and freedom from transpiration in the formation of water leaves. This theory is strengthened by the experimental production of air leaves in concentrated solutions of potassium chloride or of calcium nitrate, the high osmotic pressure of the medium having the effect of transpiration in increasing the concentration of the cell sap, precisely as in *Stigeoclonium*. Why the dissected form should result if the cell sap is dilute, and the entire form if it is more concentrated, cannot now be told, the exact mechanics of form changes being but little understood.

While the cells in *Stigeoclonium* are almost always plastic, the leaf of *Proserpinaca* loses its plasticity after attaining a length of three or four millimeters, the form then in development continuing to maturity regardless of habitat changes. Furthermore, some leaves appear to be fixed from the outset, those following the cotyledons and those developing on horizontal autumnal shoots being dissected, while the late stem leaves are likely to be entire regardless of environment. More puzzling still is *Sium* in which the cotyledons are followed by palmate leaves of mesophytic aspect, regardless of conditions, these being followed by dissected pinnate water leaves, and later by simply pinnate air leaves. The submergence of an old plant results not in the development of dissected pinnate water leaves, but of palmate leaves like those first appearing in the seedling. In the water lilies both submersed and floating leaves are developed in the water, so that variations in the water relation hardly can be assumed to be causative factors, as in *Proserpinaca*.

Observations like those noted in the preceding paragraph have led to the theory that the plasticity of amphibious plants is more apparent than real, the phenomena of leaf variation representing mere stages in development. The palmate leaves of *Sium* and the narrow submersed leaves of *Sagittaria* and of *Castalia* from this viewpoint are regarded as *juvenile* leaves, while the pinnate leaves of *Sium*, the floating leaves of *Castalia*, and the sagittate air leaves of *Sagittaria*, are supposed to be *adult*. The theory has been carried even farther, representing that the stages in the life of the individual (the ontogeny) repeat similar stages in the life of the race (the phylogeny), illustrating what is known as *recapitulation*. For example, a remote ancestor of *Sium* might be imagined to have been a palmate-leaved mesophyte, and a more recent ancestor, a pinnately dissected hydrophyte, while the present species might be regarded as an amphibious plant tending once more toward mesophytism. However, there is no valid reason for supposing that juvenile leaves, if indeed such terms as juvenile and adult represent the facts, can furnish a trustworthy clue to ancestral adult forms.[1] Various

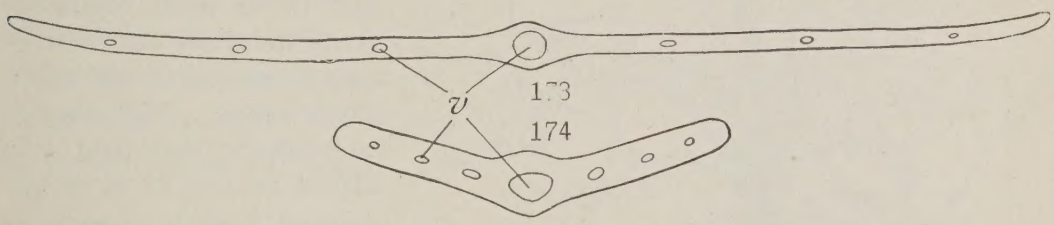
[1] A more tenable theory than that of recapitulation is the *repetition* theory, which represents that present juvenile stages repeat the juvenile stages of ancestral forms; even here it is to be recognized that juvenile as well as other stages are subject to evolutionary modification. If a present juvenile stage happens to resemble an ancestral adult stage, it means merely that the ancestral form, as compared with the present form, changed but little in passing from youth to maturity. In many cases, as in *Proserpinaca*, it is thought that the juvenile leaves differ greatly from ancestral adult leaves.

factors may induce the replacement of the adult by the juvenile state, a phenomenon known as *rejuvenescence*. This is not regarded as a reaction to a new condition, but as an indication of a sudden shock, which causes the plant to return to a youthful stage. External factors determine when, but not what, the change shall be. The development in *Sium* of mesophytic juvenile leaves rather than of dissected leaves, when an adult stem is placed in water, is cited as supporting the rejuvenescence hypothesis.

The rejuvenescence theory, at best, is a statement of facts rather than an explanation, and is likely to obscure the truth. To say that a change in form is due to rejuvenescence, is merely to say that it is due to unknown causes, the latter statement being less misleading than the former. But in such a plant as *Stigeoclonium*, or even *Proserpinaca* at certain stages, it is scarcely correct to speak of rejuvenescence, inasmuch as definite external factors produce definite results, obliterating any supposedly normal succession of stages. In the poison ivy the juvenile stage may be eliminated even in the seedling, if the developing plant is well nourished. Here and in *Castalia* and *Sagittaria*, where water as a formative factor appears to be replaced by the complex of factors known as nutrition, the assumption of such a complex is preferable to the assumption of rejuvenescence, particularly because future researches may analyze nutrition into its component factors.

The advantages of leaf variation in amphibious plants. — The striking plasticity of amphibious plants has led to a search for marked advantages in the different forms produced, but no such marked advantages are known, nor is there any satisfactory proof that the reactions are adaptive. The structural features of the two forms clearly are beneficial, the water leaf often having capacious air spaces and epidermal chlorophyll, while the air leaf has small air spaces and abundant stomata. In those forms with dissected water leaves, features that have been suggested as advantageous are the filtration of light rays, an easy yielding to currents, and a relative increase of absorptive area. If such water leaves as those of *Sagittaria* are due to poor nutrition, their form scarcely would be imagined to have advantageous significance. As to air leaves, so far as they are expanded (as in *Sagittaria*), they favor increased synthesis, while so far as they are small and compact (as in *Proserpinaca*), they are suited for low transpiration. The dying of air leaves in water or of water leaves in air is due, more probably, to lack of fitness in leaf structure than in leaf form.

Form variations in land plants. — *Variation in leaf size and proportion.* — The most universal and best understood of form variations are not those involving notable changes in shape, but those in which the changes are chiefly of size and proportion. As previously shown, xerophytic or sun leaves differ from mesophytic or shade leaves in that they are considerably smaller and thicker. Not only do these differences characterize xerophytic species on the one hand and mesophytic species on the other, but there are also many plastic species (as *Tilia americana*, *Rhus toxicodendron*) in which such differences are induced readily by growing the plants in different environments. When *Tropaeolum* is grown in dry air and dry soil, the leaves are much smaller and thicker than in moist air and moist soil, those in the latter not infrequently being five times as large as those in the former. Smaller leaves develop when the soil is dry and the air moist than when the soil



FIGS. 173, 174. — Diagrammatic cross sections of harebell leaves (*Campanula rotundifolia*): 173, a mesophytic leaf from a moist shaded habitat; 174, a xerophytic leaf from a dry sunny habitat; note that the xerophytic leaf is much the narrower and thicker; *v*, veins; considerably magnified.

is moist and the air dry, appearing to indicate that diminished absorption outweighs increased transpiration as a size-reducing factor. Many species behave in a similar though less striking manner (figs. 173, 174). Even such succulent plants as *Sedum* and *Sempervivum* may develop thin, expanded leaves in moist air.

Not only may small, thick leaves be developed where the air and the soil are dry, but also in the presence of any factor that impairs root absorption. For example, it has been shown in the case of more than two hundred species that portions of the same individual plant develop more xerophytic leaves when grown in alpine regions than when grown in the lowlands (figs. 175, 176; also figs. 358, 359); this result doubtless is due in part to reduced absorption on account of low temperature and perhaps in part to increased transpiration. Similar results have been obtained in maritime cultures, absorption being impaired by the presence of sodium chloride, and in bog cultures, where the fact of impaired absorption is variously explained; the small, thick

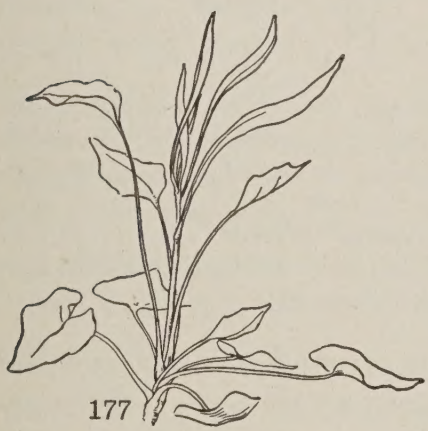
leaves of a bog individual of *Ledum groenlandicum* contrast strikingly with the large, thin leaves of a forest individual. The maritime forms of many species have thicker leaves than do the inland forms, chiefly by reason of greater palisade development.

FIGS. 175, 176. — Experimental variation in the dandelion (*Taraxacum officinale*); 175, a plant grown in a lowland garden, having large and relatively thin leaves and long scapes (*s*); 176, a plant grown in an alpine garden (originally a portion of the same individual as 175), having small and relatively thick leaves and short scapes (*s'*); note that the root and the inflorescence are much less reduced than are the other organs; both figures are drawn to the same scale. — From BONNIER.

The theory above outlined may be called the water theory of leaf size and proportion, since the absorption and the evaporation of water appear to be controlling factors. There is another prominent theory, however, in which light is regarded as the dominant factor. Adherents of the light theory speak commonly of sun and shade leaves rather than of xerophytic and mesophytic leaves. While there is no evidence that light is a direct factor, it is of undoubted indirect importance through its influence both upon carbohydrate synthesis and upon transpiration. Increased synthesis implies increased available food for leaf construction, and hence, probably, results in increased size, while increased transpiration, as has been seen, results in decreased size. The simplest situation is in the water, where synthesis is unhindered by transpiration, and here (as has been noted for *Sagittaria* and *Castalia*) the smallest leaves develop where the light intensity is least. In air leaves synthesis, and therefore the food available for leaf construction, increases as the light increases to a certain optimum, beyond which there is a decrease. Thus, intense direct light in contrast with diffuse light opposes the development of expanded leaves, partly, perhaps, because of less available food, but much more, probably, because of increased transpiration. Maximum leaf size appears to be found in the moist tropics, where transpiration is low, and yet where there is sufficient light for the optimum of synthesis. It is believed usually that a moderate increase of carbon dioxide favors an increase in leaf size; indeed, the luxuriance of Carboniferous vegetation often has been ascribed to a supposed abundance of this gas. However, a large

increase in the percentage of carbon dioxide has been shown to result in decreased leaf size.

It would seem that the chief determining factors of leaf size and proportion are those that control the water supply. High transpiration, whether caused by dry air, wind, light, or high temperature, and low absorption, whether caused by dry soil, soil salts, low oxygen pressure, or low temperature, are undoubtedly the dominating influences in determining the small size and the great thickness of the xeromorphic leaf. Furthermore, a combination of factors is more effective than any single factor, both as to the rapidity of development and as to the degree of xeromorphism attained; an



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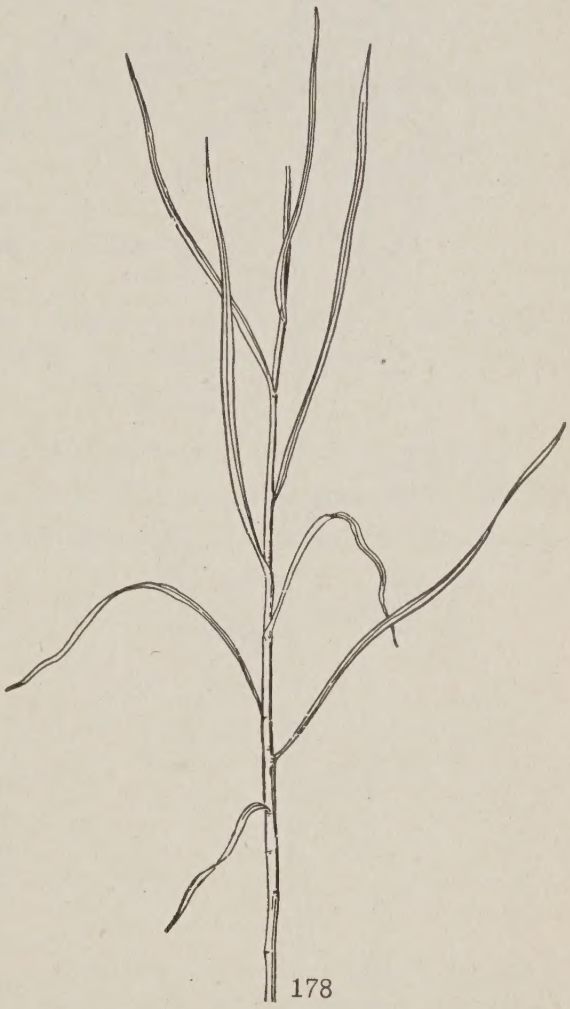

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FIGS. 177, 178. — 177, a young mesophytic individual of the harebell (*Campanula rotundifolia*), showing leaf variation; note the broad basal leaves and the narrower stem leaves; 178, the upper portion of a xerophytic individual of the harebell (*Campanula rotundifolia*); showing the characteristic linear stem leaves.

" alpine " leaf, for example, is produced most quickly by exposing a plant to intense sunlight, high temperature, and dry air by day, and to low temperature by night. The large size and the thinness of the mesophytic leaf, on the other hand, are due to the less extreme influence of the factors (transpiration, heat, light, etc.) producing the xeromorphic leaf, supplemented by the optimum amount of light and

carbon dioxide for synthesis. In the xeromorphic leaf there is a relatively large amount of cell division parallel to the surface, resulting in dorsiventral enlargement, while in the mesophytic leaf, surface enlargement results from the extensive lateral development of the individual cells supplemented sometimes by an increased number of cell divisions perpendicular to the surface.

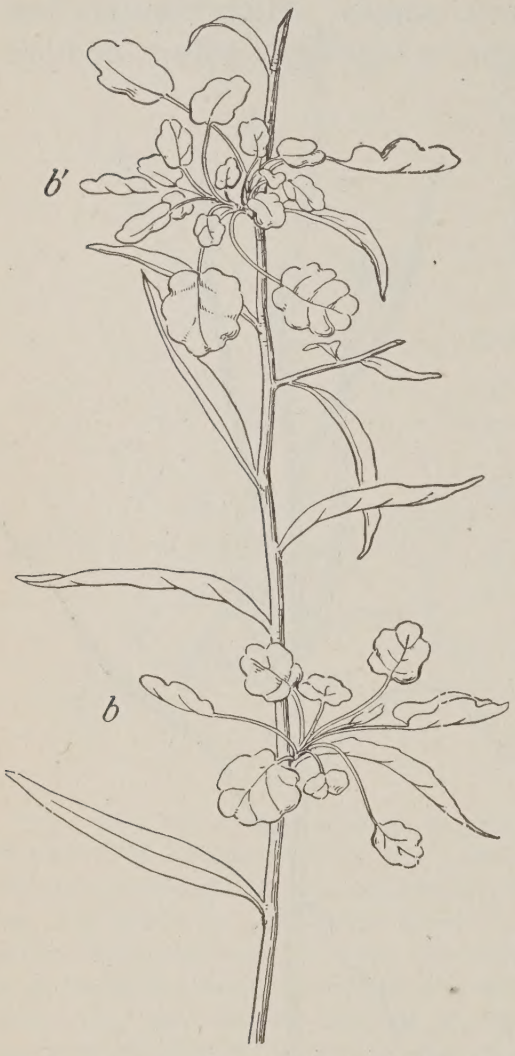
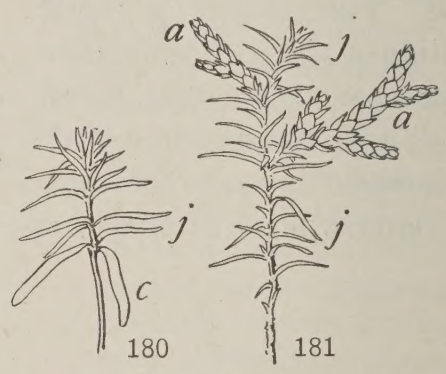


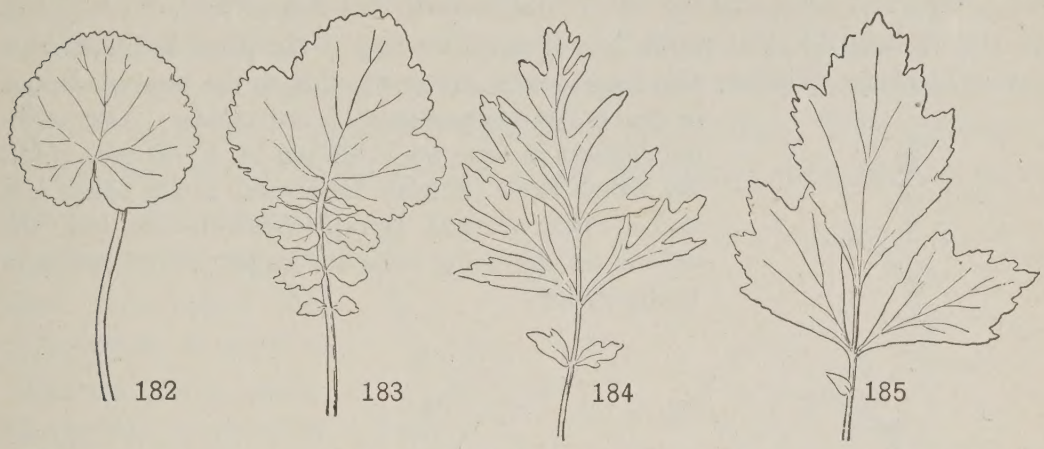
FIG. 179. — Leaf variation in the harebell (*Campanula rotundifolia*); the apex of the shoot has been cut off, and lateral buds have developed at *b* and *b'*; note that the first leaves of the axillary rosettes are short and roundish, as in seedlings and basal rosettes; such an occurrence sometimes is called a reversion to a juvenile stage. — From FAMILLER.

Variation in the leaf contour of land plants. — The harebell (*Campanula rotundifolia*) has a basal rosette of petioled, round, or ovate leaves, while the upper stem leaves are narrowly lanceolate or even linear (figs. 177, 178). Early experiments related these leaf variations to light, the large basal leaves being thought to result from shade or diffuse light, and the narrow upper leaves from intense light. However, the basal leaves are round on exposed rocks, and the stem leaves are nearly as narrow in the shade as in the sun. Both in sun plants and in shade plants there is a gradation from broad basal leaves to narrow stem leaves,



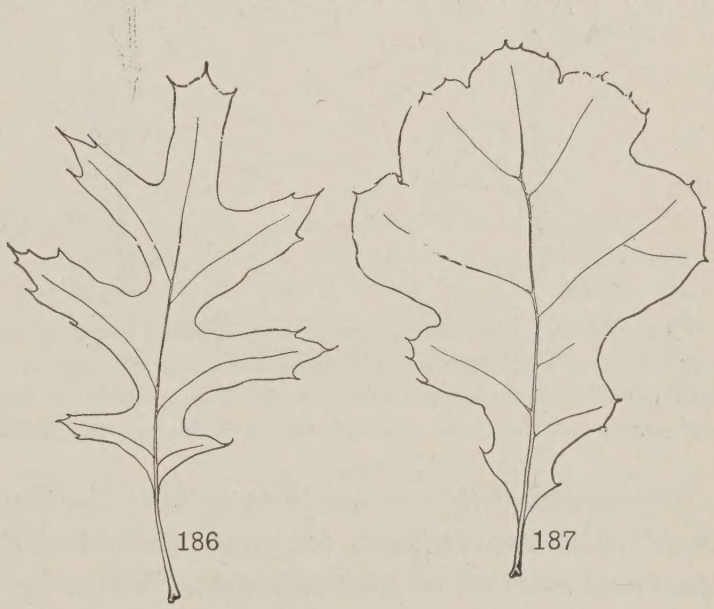
FIGS. 180, 181. — Leaf variation in the arbor vitae (*Thuja occidentalis*); 180, a seedling, showing the cotyledons (*c*) and the awl-shaped "juvenile" leaves (*j*); 181, an older plant, showing "juvenile" leaves (*j*) and the first lateral branches bearing scale-shaped "adult," leaves (*a*).

the chief difference being that at any given node the leaf of the sun plant is narrower and thicker. If the terminal shoot is removed,



FIGS. 182–185. — Leaf variation in *Geum virginianum;* 182, a basal leaf from a winter rosette; 183, a higher leaf from a winter rosette; 184, a leaf from the lower part of a stem; 185, a leaf from the upper part of a stem.

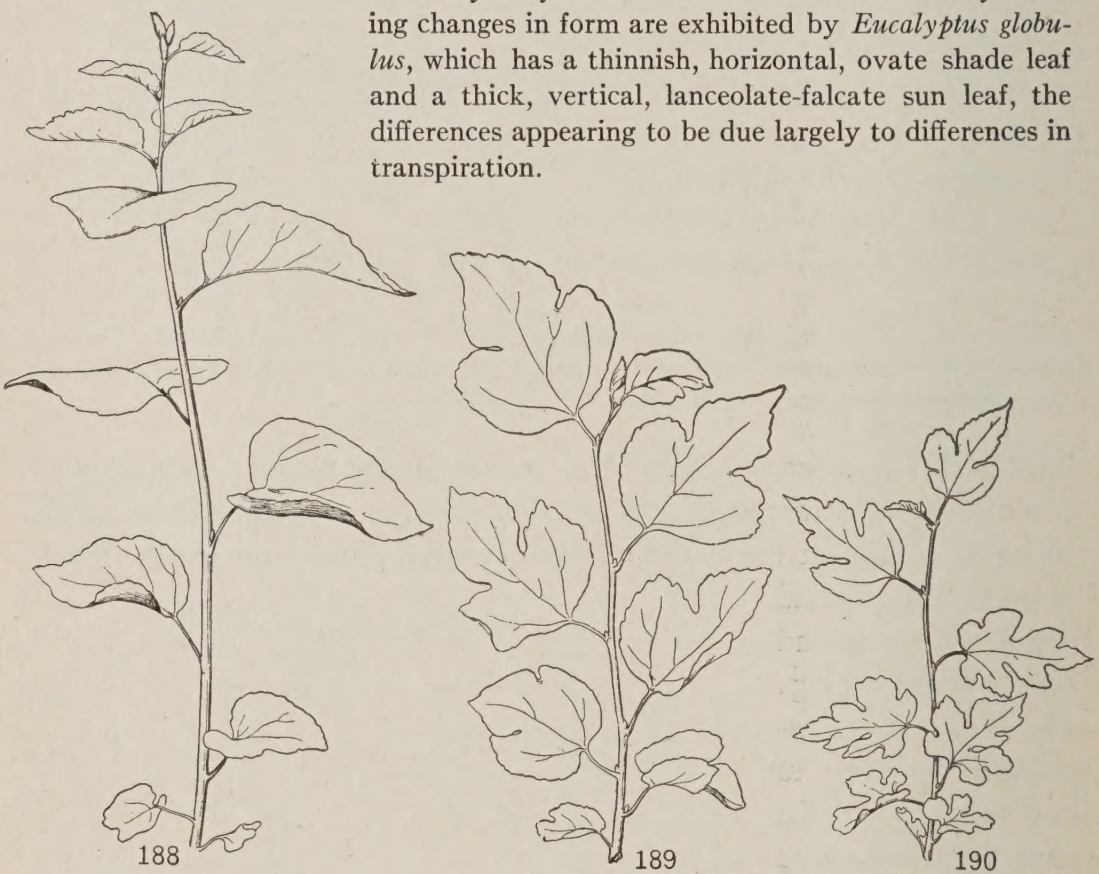
lateral shoots develop, their first leaves being round, regardless of conditions. Furthermore, any sudden change, even that from shade to light, results in the arrest of the terminal shoot and in the development of lateral shoots with round basal leaves (fig. 179). Thus, *Campanula* appears to resemble *Sium* in that there is a more or less fixed succession of leaf forms, any shock to the plant causing "rejuvenescence."



FIGS. 186, 187. — Leaf variation in the black oak (*Quercus velutina*); 186, an upper leaf, exposed to strong sunlight; 187, a shade leaf from a lower branch of the same tree; leaves resembling 187 especially characterize basal shoots (suckers).

Variations comparable to those of *Campanula* are exhibited by *Satureja glabra* (figs. 293–296) and by various species of *Arabis* and *Lechea*. In *Nicotiana* (fig. 89) and in many similar plants there is a very gradual change from the base to the apex of the stem, the leaves becoming progressively smaller, shorter, and thicker, as well as more erect; the changes in

transpiration from the base to the apex probably suffice in large part to explain such cases.[1] In *Thuja* (fig. 180) the first leaves are needle-shaped, as in the juniper, but after a year or two there appear flattened lateral branches with appressed awl-shaped leaves (fig. 181). Thenceforth awl-shaped leaves continue to develop through life, but needle leaves again develop if the plant is placed in a moist chamber. Whether this represents a direct reaction to the new conditions or merely " rejuvenescence " is not known. Very striking changes in form are exhibited by *Eucalyptus globulus*, which has a thinnish, horizontal, ovate shade leaf and a thick, vertical, lanceolate-falcate sun leaf, the differences appearing to be due largely to differences in transpiration.

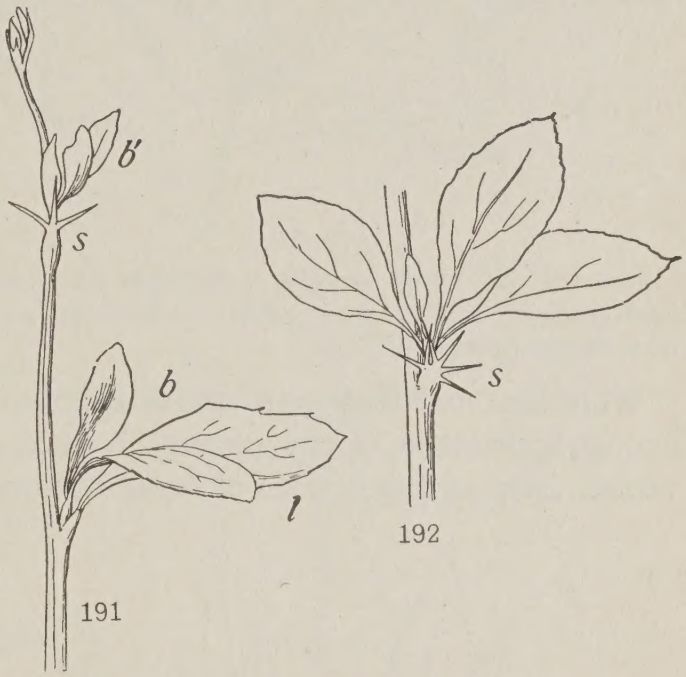


FIGS. 188–190. — Shoots of a mulberry (*Morus*), showing leaf variation; 188, a vigorous vertical shoot, showing relatively entire leaves spirally arranged on the stem; 189, a horizontal shoot with leaves somewhat lobed and all in one plane facing the light, as a result of stem and petiole twisting; 190, a shoot similar to 189 but with smaller and more lobate leaves.

In *Geum virginianum* and *Ranunculus abortivus*, and in many similar plants, the leaf changes are more complicated than in *Campanula*, the basal rosettes of roundish winter leaves being succeeded by variously divided stem leaves; in *Geum* the round leaves are followed by pinnate and later by three-parted leaves (figs. 182–185). In *Silphium laciniatum*, narrow, undivided early leaves are followed by broader, much-lobed adult leaves. In various oaks not only are the early leaves

[1] In some plants, as the cottonwood, the upper leaves are larger than the lower, appearing to be better nourished.

relatively entire and the later leaves lobed, as in *Geum*, but the upper leaves are more lobed than the lower, whatever their time of appearance, while leaves on vigorous young shoots (such as stump suckers) are scarcely lobed at all (figs. 186, 187). Perhaps the lobation of the upper leaves, as well as their smaller size and greater thickness, is due to the smaller water supply to which they are subject. The large leaves of vigorous suckers also appear better nourished than do the other leaves. These observations would suggest that the lobed leaf represents a sort of skeleton, which, under favorable vegetative conditions (*e.g.* freedom from excessive transpiration or good food supply), may become filled out into an entire leaf.

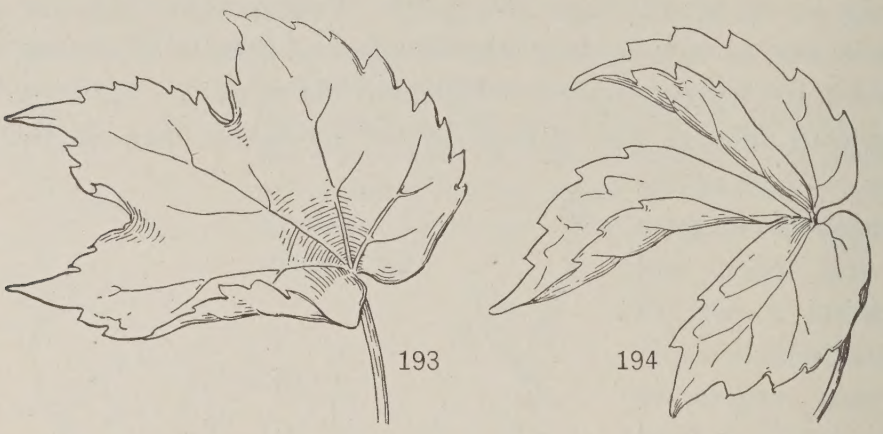


FIGS. 191, 192. — Leaf variation in the barberry (*Berberis vulgaris*); 191, a young shoot whose lower bud (*b*) is subtended by an ordinary foliage leaf (*l*), while the upper (*b'*) is subtended by a spine (*s*); the leaf and spine are homologous (*i.e.* similar in position) and develop from similar primordia); 192, a bud similar to *b'* in 191 but somewhat older.

This view, perhaps, is supported by the fact that various leaves (as in *Ricinus*) are more divided in youth than at maturity, the regions between the principal veins developing last. If such leaves while young were exposed to higher transpiration or to decreased food supply, they probably would remain in the more lobate condition. In the mulberries the more lobate leaves usually are small and on slender branches (as if poorly nourished), while the simple leaves commonly are larger and on more luxuriant shoots (figs. 188–190). Early in the year the leaves of the staminate tree may be larger and more entire than are those of the pistillate tree, perhaps because in the latter the food otherwise available for leaf construction is utilized in fruit development. In the barberry there are gradations between ordinary leaves and leaf skeletons which are reduced essentially to spines (figs. 191, 192), and it is possible that the latter are due to poor nutrition or perhaps to excessive transpiration (see discussion of stem spines, p. 256).

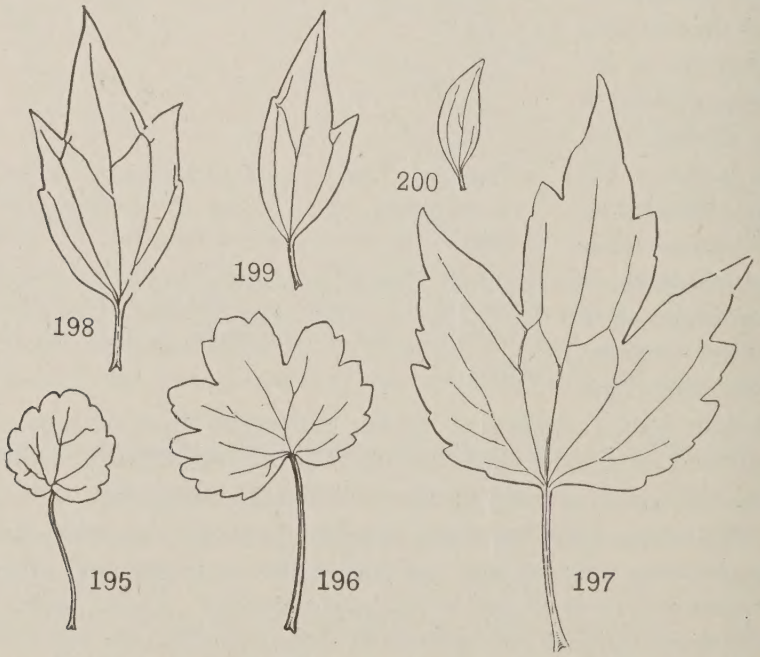
While the compound air leaves thus far considered differ from divided water leaves in appearing where transpiration is high, rather than

where it is low, in each case their development seems to be associated with poor nutrition. The lack of rigorous experimental data forbids further analysis, and makes dubious even the suggestions here given.



FIGS. 193, 194. — Leaf variation in the Japan ivy (*Psedera tricuspidata*); 193, a three-lobed simple leaf from the upper portion of a vine; 194, a compound leaf with three leaflets from the lower portion of a vine.

While the *Campanula* and *Geum* categories of leaf variation are poorly enough understood, chiefly, perhaps, because of inadequate experimentation, there are many cases of changing form that are not understood



FIGS. 195–200. — Leaf variation in the motherwort (*Leonurus cardiaca*); 195, a basal rosette leaf; 196, one of the more apical rosette leaves; 197, a leaf from the lower part of a stem; 198, 199, leaves from the upper part of a stem; 200, a leaf from the floral region; note that lobation and leaf size increase for a time, culminating in 197, and reaching a minimum in 200.

at all. In a number of plants (as *Lepidium*, *Lactuca*) the large, thin, rosette leaves are more divided than are the small, thick, stem leaves. In *Cytisus scoparius* the three-lobed lower leaves are followed by simple (or more correctly, one-lobed) leaves, greatly reduced in size, and in the Japan ivy the lower leaves are three-parted, while the upper leaves are simple (though with similar palmate venation) and often as large as or even larger than those below (figs. 193, 194). In *Leonurus cardiaca* the intermediate stem leaves are more divided than are those below or above (figs. 195–200), and in *Sassafras* almost any leaf may be entire or variously lobed, apparently without relation to transpiration or nutrition, or even to the phenomena of rejuvenescence. One of the most extraordinary cases of leaf dimorphism is exhibited by the staghorn fern (*Platycerium*), in which there are erect leaves that bear the sporangia, and sterile leaves that adhere closely to the ground and keep the substratum constantly moist. The sterile leaves appear to react to contact and gravity rather than to light, ultimately forming an overlapping series, the lowermost of which gradually become transformed into humus.

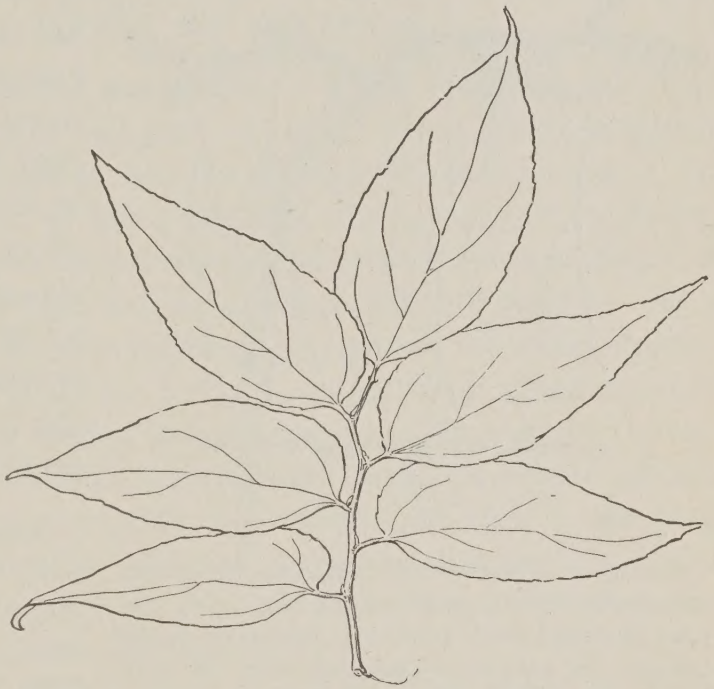


FIG. 201. — A horizontal shoot of the hackberry (*Celtis occidentalis*), showing leaf asymmetry; note that the leaves form a "mosaic," the expanded portion of the base of one blade coming into juxtaposition with the contracted portion of the base of the adjoining blade; all the leaves are in one plane by reason of stem twisting or petiole growth.

The advantages of leaf variation in land plants. — In so far as the basal or lower stem leaves of any plant are large and thin, they favor the optimum of synthesis, while in so far as the upper leaves are small and thick, they are protected from excessive transpiration. In essentially all of the contour categories noted, that of *Lepidium* with com-

pound basal leaves, as well as that of *Campanula* or *Geum* with simple basal leaves, these differences in size and thickness obtain, and the advantages follow as cited. Advantages from differences in contour, however, are not so obvious. It often is assumed that each of these differences is beneficial, and that the very fact of change, whether from without or from within, is *prima facie* evidence of usefulness. But attempts to discover advantages have met with failure. It is true that compound leaves have been thought to be useful in the sifting of light (p. 66), but many plants (as *Lepidium*) have their compound leaves below, and in no case is there evidence that the capacity of leaves to sift light has had much effect upon the survival of species. Probably contour variability in leaves is of no special import in determining the success or failure of plants.

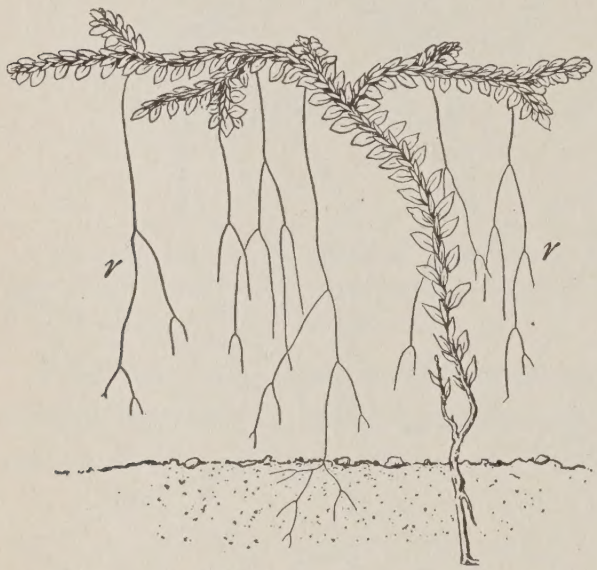


FIG. 202. — A plant of *Selaginella apus*, illustrating anisophylly (*i.e.* inequality in leaf size); note that large and small leaves adjoin one another in regular fashion; the structures depending from the horizontal stems are rootlike organs known as rhizophores (*r*); note the dichotomous branching.

Asymmetry and anisophylly. — In certain plants (as *Celtis* and *Begonia*) the leaves exhibit *asymmetry*, the basal region bulging more on one side than on the other, giving a general oblique effect (fig. 201). It has been shown in a number of instances that leaf asymmetry is due to unequal illumination, the bulged portion having received more light in its development, because of its more favored position. The smaller portion commonly develops close to the stem and often is shaded by the next leaf. Probably the light influence is indirect (*i.e.* affecting synthetic activity) rather than direct. By twisting a petiole or by making incisions so as to check the water supply, it is possible to produce in *Begonia* a symmetrical leaf or even a leaf in which the basal asymmetry is reversed, while leaves commonly symmetrical in like manner may be induced to become asymmetrical. *Anisophylly* is well illustrated by such a plant as *Selaginella* (fig. 202), which has two sorts of leaves, large and small, more or less regularly placed in relation to each other, and also by the leafy liverworts, which have two dorsal rows of green leaves and a ventral row of small, colorless leaves (*amphigastria*). Anisophylly, like asymmetry, is believed to be due to the unequal action of various factors, among which light and gravity appear the more important. In many plants anisophylly characterizes the leaves of horizontal shoots, where the influ-

ence of such factors is unequal, while the leaves of erect shoots are equal. In some cases at least, the primordia of anisophyllous leaves are equal, and it has been shown that upon emergence from the bud, one leaf of a pair has a more favored position and hence manufactures more food than does the other, making possible its greater development. In some plants anisophylly seems unrelated to external factors. Both asymmetry and anisophylly have been considered advantageous from the standpoint of light-reception, since they favor the development of leaf mosaics and the maximum utilization of space.

7. THE ABSORPTION OF WATER AND OF NONGASEOUS SOLUTES BY LEAVES

General remarks on leaf absorption. — While roots are the chief regions of entry for water and salts, there are many plants in which these substances enter directly into the chlorophyll-bearing organs. In such cases the division of labor between absorptive and synthetic organs is not pronounced, and there may be little or no transportation of water and salts through a specialized conductive system. As a class, however, leaves are disadvantageously placed for water absorption, since they are in much less frequent contact with water than are roots, and generally are subject to transpiration rather than to absorption; the cutinized epidermal walls of most leaves, which are advantageous in checking transpiration, are equally effective in checking absorption. Where the outer walls are of cellulose, absorption and also transpiration may take place, so that leaf absorption is advantageous chiefly where transpiration is low or wanting.

Absorption by chlorophyll-bearing organs in water plants. — *Algae and bryophytes.* — In nearly all water plants the outer walls are of cellulose, and, since there is constant water contact and freedom from transpiration, no conditions are more suitable for water absorption by chlorophyll-bearing organs. In many algae there is a homogeneous green body which absorbs water through its entire surface. In other forms, as in *Chara* and *Bryopsis* (figs. 381, 382) and in large marine algae (fig. 52), there are holdfasts which function as anchorage organs. Probably the holdfasts are permeable, but the much more extensive chlorophyll-bearing portion with its permeable walls is vastly more important from the standpoint of absorption. The aquatic liverwort, *Riccia fluitans*, has a homogeneous green body without rhizoids, its mode of absorption being comparable to that of algae with similar aspect. In aquatic mosses (as in *Fontinalis*) water probably enters chiefly through the leaf surfaces.

Vascular plants. — There are some rootless aquatic ferns and seed plants in which all water and salts must enter through the leaf or stem surface, as in *Utricularia vulgaris* (fig. 215) and in *Ceratophyllum.* In *Salvinia* there are synthetic floating leaves and absorptive water leaves, the latter being finely dissected and quite unlike ordinary leaves (fig. 203). In *Wolffia* (fig. 315) there is a thalloid body, of which the submersed lower part is a region of absorption, while the emersed upper part is a region of synthesis and gas exchange. Most submersed seed plants, however, have soil roots, so that experimentation is necessary to determine the absorptive region. The presence of cellulose epidermal walls and of a slightly developed conductive system has led to a general belief in the dominance of leaf absorption.

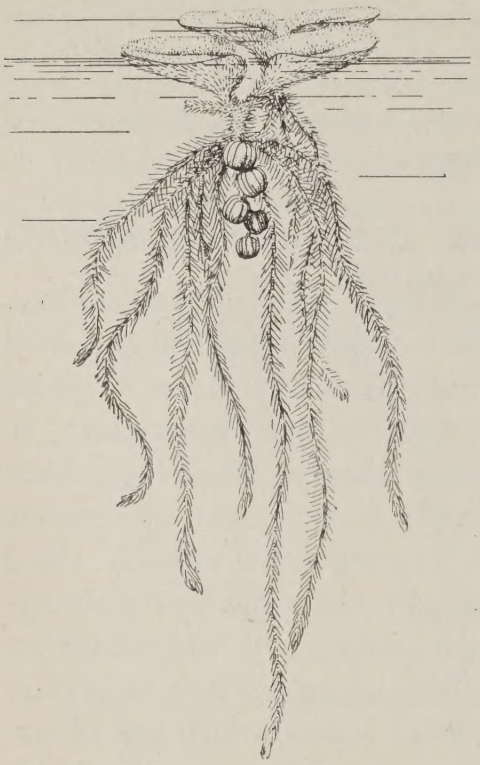


FIG. 203. — A plant of *Salvinia natans,* showing the broad floating leaves, whose upper surfaces have aerial relations, and the dissected, descending submersed leaves, which absorb water and salts from the medium and which bear reproductive organs; note the abundant leaf hairs. — From COULTER (Vol. One).

That in attached submersed plants root absorption is not inconsequential has been shown in some instances, lithium salts having been supplied to the medium around the roots and later detected in the plant, and the ascent of water in the conductive tract has been observed; the abundant development of root hairs in many instances and the greater luxuriance of plants in loam than in gravel also appear to argue for root absorption. However, there is scarcely any doubt that in water plants leaf absorption generally is much greater in amount than is root absorption, though it is likely that plants differ in respect to the relative importance of the two; for example, *Potamogeton* may depend more upon root absorption than does *Elodea,* since it grows less readily in an aquarium without a soil substratum. Leaf absorption would seem the more advantageous, since it does not involve the development of a conductive tract and the consequent translocation of water.

Absorption by chlorophyll-bearing organs in land plants. — *Algae and lichens.* — Some green algae (as *Vaucheria*) and various blue-green algae form felts on moist soil, the entire surface being absorptive, as in

water forms; here the wet soil may provide constant water contact, though transpiration at times may be excessive. No group illustrates absorption by the chlorophyll-bearing organs better than do the lichens. For example, the reindeer lichen (*Cladonia rangiferina*, fig. 204), which is stiff, brittle, and gray when dry, becomes soft, flexible, highly elastic, and green when wet, by reason of the large amount of water it is able to absorb. Upon entering the lichen, the water passes rapidly by capillarity between the hyphae and more slowly through the cell membranes and lumina. Lichens as a class are exposed to strong transpiration, and soon lose most of the water that is so quickly absorbed.

Bryophytes. — Probably all mosses and liverworts are able to absorb water through chlorophyll-bearing organs, whenever they are moistened by rain or dew. In some leafy liverworts water catchment and absorption are facilitated by a cuplike arrangement of the leaves, but

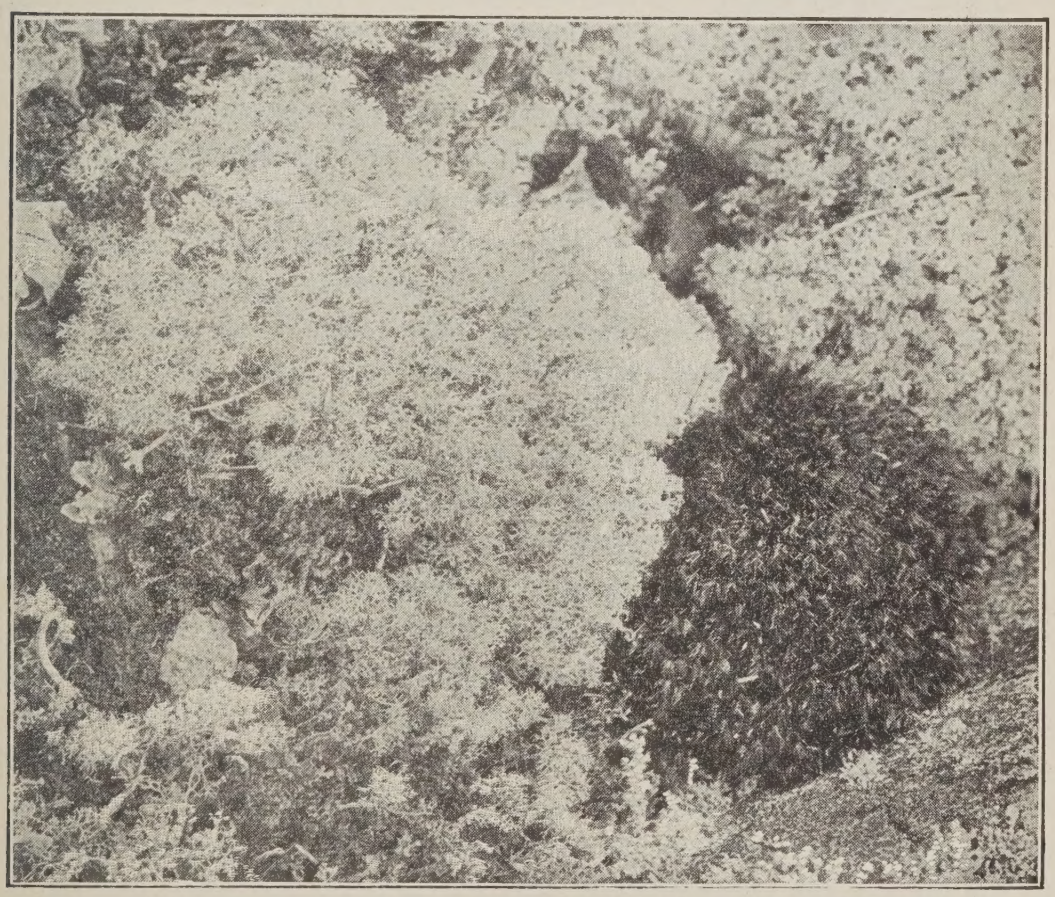


FIG. 204. — Cushion plants, which absorb water readily through the aerial organs; the light-colored cushions are reindeer lichens (*Cladonia rangiferina*), and the dark-colored cushion is a moss, *Bartramia pomiformis;* Grand Marais, Minn. — From MACMILLAN.

most liverworts and many trailing mosses (as species of *Hypnum*) grow so near the substratum that water absorption generally is possible without special structural arrangements. The situation is different in erect mosses with more or less solitary stems (as *Polytrichum*, *Catharinea*, *Climacium*), in which rhizoid absorption probably exceeds leaf absorption in amount, the latter being confined chiefly to periods when the leaves are moist from rain or dew; in addition to lessened opportunity for leaf absorption, such mosses also are exposed to greater transpiration than are mosses in general. In other mosses and liverworts rhizoid absorption probably supplements leaf absorption, but it is probable that in most cases the latter exceeds the former (p. 33).

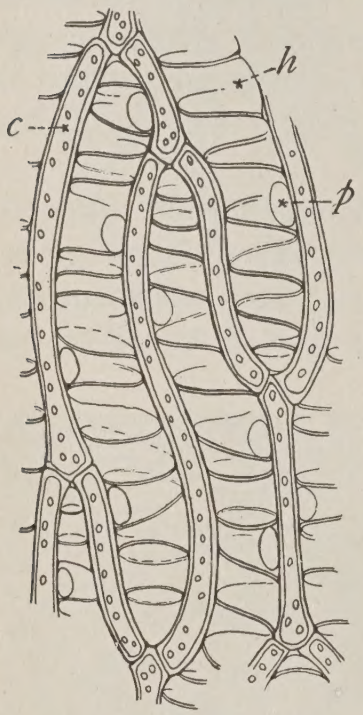


FIG. 205. — A surface view of a part of a leaf of *Sphagnum*, showing the narrow, elongated living cells (*c*) containing chloroplasts, and the larger, colorless dead cells (*h*) with their spiral thickenings and pores (*p*); highly magnified. — From COULTER (Vol. One).

Remarkable cases of leaf absorption are afforded by various mosses that grow in dense *cushions* (as *Dicranum*, *Leucobryum*, *Sphagnum*, fig. 204). Such cushions may be regarded as systems of capillaries connected with the substratum; thus a constant supply of water is available for the leaves, except in very dry weather. Since each year the individual stems of a cushion grow at the apex and die at the base, it is unlikely that the soil rhizoids are of any significance in absorption, at least after the cushion is a few years old; the aerial rhizoids that develop in some species probably facilitate capillary activity. The most noteworthy of the cushion mosses is the peat moss, *Sphagnum*, in which capillary phenomena are facilitated further by drooping lateral branches (fig. 285), and especially by the presence of dead air-containing cells with porous, fiber-thickened walls intercalated regularly among the synthetic cells (fig. 205). Not only do these dead cells fill with great rapidity, but the presence of porous cell walls in the stem gives the plant an internal capillary system which supplements the external capillary system possessed in common with other cushion mosses.

Leucobryum much resembles *Sphagnum*, except that porous dead cells form external absorptive layers comparable to an absorptive epidermis (as in orchid roots), the chlorophyll-bearing cells occupying the median region of the leaf (fig. 206). The dry dead cells cause the characteristic white aspect of the moss (whence the name, *Leucobryum*, *i.e.* white moss). Interesting capillary phenomena of quite another sort are exhibited by *Polytrichum*, a moss whose leaves become closely appressed to the stem during dry weather; if the base of such a stem is placed in water, the leaves open out almost instantly by reason of the capillary ascent of water along the dry sheathing leaf bases and between the chlorenchyma plates of the leaves (figs. 207, 208). Doubtless much water enters in this manner, thus supplementing ordinary leaf and rhizoid absorption.

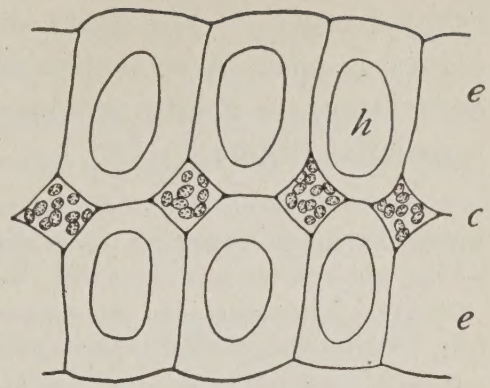
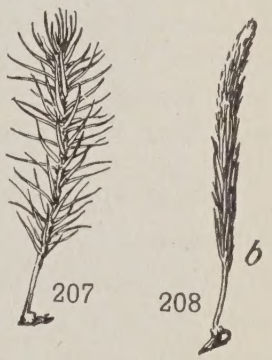


FIG. 206. — A cross section of a leaf of *Leucobryum*, showing the central chlorophyll layer (*c*) with its chloroplasts, and the peripheral layers (*e*) whose cells communicate with one another by means of the pores (*h*) that perforate the walls; highly magnified.

As in the air roots of orchids, the absorptive process in lichens and in cushion mosses has two phases, the first being a capillary phenomenon, which consists of a rapid ascent of water between the stems or of a rapid filling of air spaces (or of both in *Sphagnum* and *Leucobryum*); the second phase is represented by a slow osmotic movement, as in root hairs. The water which is absorbed so rapidly by lichens and by cushion mosses is lost more slowly by transpiration, *Sphagnum* being able to absorb as much in a minute as is lost by ordinary transpiration in a week. While some cushion mosses are mesophytic (as in *Bartramia* and some species of *Dicranum*), others tend toward xerophytism (as in *Leucobryum*), and even *Sphagnum* may be called a bog xerophyte. Lichens usually are pronounced xerophytes, and (as with some mosses) absorption must be a comparatively infrequent phenomenon (particularly since only liquid water can be absorbed in quantity), while exposure to transpira-



FIGS. 207, 208. — Aspects of *Polytrichum commune*, a xerophytic moss: 207, a leafy shoot, as seen when the water supply is adequate; 208, a similar shoot that has been exposed to desiccation, the loss of water having caused the leaves to become appressed to the stem; when the base of such a shoot is placed in water, the leaves soon assume the position seen in Fig. 207.

tion is frequent.[1] For aerial absorption to be advantageous in such plants, it must be accompanied by an ability to endure prolonged desiccation, an ability possessed by lichens and by some mosses in superlative degree.

Vascular plants. — The aerial leaves of ferns and seed plants are cutinized, and water absorption commonly is so slight as to be without significance.[2] Wilted leaves, when placed in contact with water, absorb enough to enable them to recover their usual turgescence, but this phenomenon probably is of little significance in nature. Water absorption has been predicated as a function of many living leaf hairs, especially in xerophytes, largely, perhaps, because their water supply is scant, and because no other use is known for these hairs. The felted hairs of *Centaurea* have been thought to be useful in this way, since the leaf can take up thirteen per cent of its weight, when placed in water for a day. *Salt-secreting hairs*, as in *Reaumuria*, have been shown to absorb water. Recent experiments show that xerophytic leaves as a class possess less capacity for absorption than do leaves in general, any water taken up being lost with rapidity, since it does not penetrate to the living cells. Nor should leaf absorption be expected *a priori*, above all in xerophytes, since a cutinized epidermis is as effective in keeping water out as in keeping it in. It has been shown that such salt-containing plants as *Salicornia* are able to absorb water somewhat readily through the aerial organs. Though adequate experiment is lacking, there is some reason for believing that the leaf sheaths of many grasses and umbellifers and the cup-shaped leaf bases of *Silphium perfoliatum* have some absorptive efficiency.

Water absorption in epiphytes. — *Thallophytes and bryophytes.* — In regions with cold winters true epiphytes are confined essentially to the lower plants, and in these groups absorption is dominantly a function of chlorophyll-bearing organs rather than of rhizoids. The widespread distribution of these plants in exposed situations is due in large part to their ability to endure prolonged desiccation, since they quickly lose most of the absorbed water by transpiration through the surface by which it entered. Among such xerophytic epiphytes are some algae (as *Pleurococcus*) and liverworts (as *Frullania*) and many mosses (notably *Orthotrichum*), but the most representative epiphytic group is that of the lichens. Probably the most xerophytic of all plants are the *crustose lichens* (as *Buellia*), which are either epiphytic or *epilithic* (*i.e.* growing on rocks), appearing embedded within the substratum. Most crustose lichens absorb water chiefly through

[1] Experiments appear to show that certain mosses in a few seconds can absorb sufficient water vapor to increase their weight 25 to 75 per cent, and that fruticose lichens may absorb enough water vapor to be of appreciable advantage.

[2] In the filmy ferns, which are largely delicate plants of tropical forests, cutinization is slight and absorption by leaves often surpasses in amount absorption by subterranean organs.

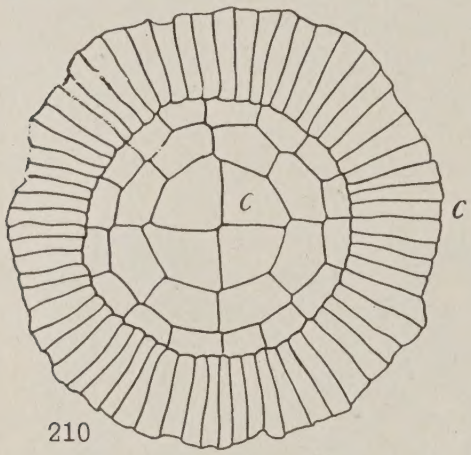
the upper surface, though some species have upper surfaces which are not readily wetted or which are covered with an impermeable crust. On dry rocks, at least, such plants absorb water chiefly during or immediately following precipitation, soon drying out again, and entering a period of inactivity; the active period may be longer in the case of bark lichens, owing to the greater reten-

FIG. 209. — A live oak (*Quercus virginiana*) festooned with the long moss (*Tillandsia usneoides*), an epiphytic member of the pineapple family, which absorbs liquid water by means of specialized scale hairs; Tampa, Fla. — Photograph by E. W. COWLES.

tiveness of the substratum. *Foliose lichens* (for example, *Parmelia;* fig. 417) are more leaflike and are attached to rock or tree surfaces by evident rhizoids; perhaps also they are less xerophytic, though capable of withstanding prolonged desiccation. Foliose lichens commonly absorb through both surfaces, but mainly through the lower surface, except in a few instances (as in species of *Parmelia* with black under surfaces). The gelatinous lichens (as *Collema*) absorb great quantities of water and remain for some time as mucilaginous masses. Possibly the rhizoids supplement the chlorophyll-bearing organs in absorption, but to what extent if any is unknown. Some mosses (as

Andreaea and *Grimmia*) are epilithic xerophytes and withstand prolonged desiccation without harm, reviving rapidly during rain as a result of leaf absorption.

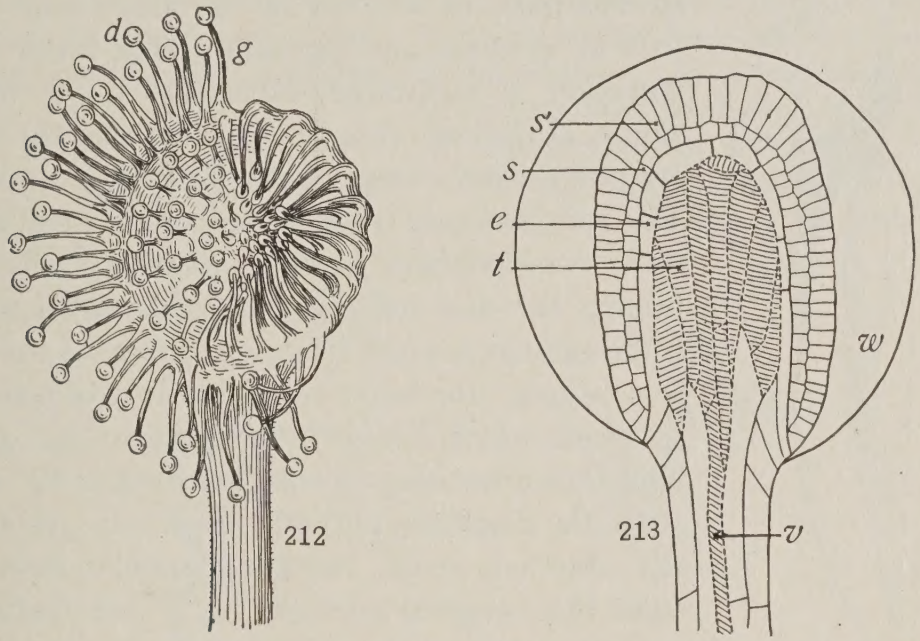
Bromeliaceae. — The most remarkable instance among seed plants of absorption by aerial leaves is in the Bromeliaceae, a family of tropical epiphytes, represented in the southern United States by *Tillandsia*, especially *T. usneoides*, the "long moss," a rootless plant with minute leaves (fig. 209). In these epiphytes the chief organs of absorption are specialized hairs, with which the long moss, for example, is completely covered; that these plants do not depend upon root absorption is shown by their occasional development on telegraph wires, and by the fact that they blow from place to place, continuing their activity wherever they lodge. Probably the long moss represents an extreme epiphytic form that has been derived from an ancestry similar to its relative, the pineapple; even now there exists a series of intergrading forms, those at the pineapple end of the series having ordinary absorptive soil roots and scattered or localized absorptive scales, while those at the *Tillandsia* end have only anchorage roots or no roots at all and have an abundant development of absorptive scales (fig. 277).



FIGS. 210, 211. — Absorptive scale hairs of *Tillandsia:* 210, a scale hair, as seen in surface view; 211, a scale hair, as seen in cross section; the outer cells (*c*) are dead, and absorb water readily when moistened, thus elevating the scale and opening the channel, *aa*, along which water passes by capillarity; subsequently the water enters the living stalk cells (*s*); *e*, epidermis; highly magnified.

The *absorptive scales* or scale hairs of the Bromeliaceae are epidermal structures consisting of a sunken, multicellular, thin-walled, living stalk, capped by a protruding, multicellular, shieldlike organ, whose cells are dead and have thick cellulose walls (figs. 210, 211). Liquid water is absorbed by the dry scale hairs with remarkable rapidity, but the rest of the epidermis is highly cutinized and impermeable. When the surface is moistened, the dead cells fill with water, causing an expansion of the structure which lifts it from the rest of the epidermal surface, thus making possible the movement of water along the capillary passages between the scale and the subjacent epidermis, as well as through the scale. The water then enters the living stalk cells osmotically, as in root hairs, the presence of sugar in the cells facilitating the process. When evaporation begins, the dead cells lose their water and the scale collapses, thus closing the region where capillary water enters,

and reducing the amount of water lost. It has been shown that salts as well as water may enter these plants through the scale hairs. The Bromeliaceae furnish the only conspicuous well-attested example among the higher plants of the absorption of water by aerial leaves, and the only well-attested structure in any group, which both facilitates absorption and retards transpiration. Nothing is known concerning the steps in the evolution of these hairs, and their rigidity gives little hope of obtaining through experiment a clue to their origin.



FIGS. 212, 213. — The absorptive and digestive glandular hairs of a sundew (*Drosera rotundifolia*): 212, a leaf, showing the conspicuous glandular hairs (*g*) covering the upper surface; the hairs at the right are inflected toward an entangled insect; note that the hairs are tipped by a drop of secreted liquid (*d*), which attracts insects to the leaf and also entangles them; 213, the terminal capitate portion of a glandular hair, as seen in a median longitudinal section; the conductive bundle (*v*) entering the hair from the leaf is much enlarged at its terminal portion, where it is composed of tracheids (*t*); the terminal tracheids are inclosed by the protective sheath or endodermis (*e*), outside of which are two epidermal layers of secretory cells (*s s'*); note the palisade-like nature of the cells in the outer secretory layer; *w*, a drop secreted by these layers; 212, somewhat magnified; 213, highly magnified. — 212 after KERNER, 213 after DEBARY.

Food absorption by the leaves of carnivorous plants. — *The sundews.* — A few plants possess the power of absorbing and digesting animal food. The best understood of these is the sundew, *Drosera*, a bog plant whose leaves have prominent glandular hairs, which usually are wine-red in color and tipped with viscid secreted drops that glisten in the sunlight like dewdrops (fig. 212). Insects, which make chance visits or which are attracted by the leaf brilliancy or color, are held by the viscid drops, and their efforts to escape result in contact with other drops, so that they are held still more securely. The presence of

the insect stimulates the glandular hairs to secrete more actively and also differently, the more important substances secreted being formic and other acids and *proteolytic* (*i.e.* protein-digesting) enzymes, which transform into solutes the digestible portions of the insect body. The presence of the insect further incites an incurving of the leaf margins and of the glandular hairs not originally touched, so that most of or even all the hairs may take part in secretion and digestion. The latter phenomenon is facilitated, especially if the insect alights at the leaf center, by the fact that the hairs are progressively longer from the center outward. The hair structure is somewhat complicated, there being two peripheral layers of secretory cells containing the wine-red pigment, underneath which is the endodermis and a branch of the leaf conductive system; the latter consists chiefly of a row of tracheids, which diverge in the terminal part of the hair, thus presenting an enlarged surface (fig. 213). After the digestible portions have been absorbed, the secretions cease, and the glandular hairs assume their original position. It is said that inorganic bodies, such as dirt particles, excite no enzyme secretions or leaf movements.

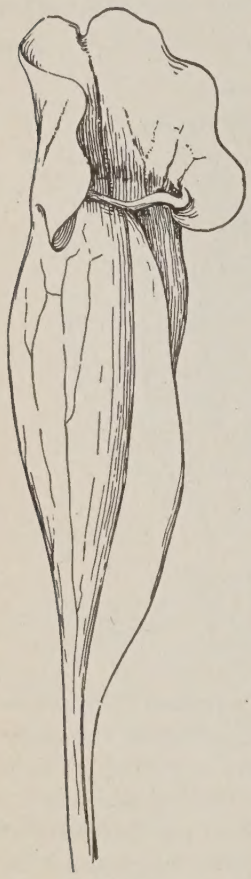


FIG. 214. — A leaf of the pitcher plant (*Sarracenia purpurea*); usually such pitcher leaves are partly filled with water into which insects often crawl or fall.

Besides the various species of *Drosera*, other members of the same family, as *Drosophyllum*, have irritable glandular hairs. Two of the most remarkable genera are *Aldrovanda* and *Dionaea*, which have sensitive leaf blades that close suddenly when irritated, and prevent the escape of alighting insects. Impact upon the stiff outer part of certain hairs is perceived by delicate cells beneath and transmitted to the region where movement is effected. The secretion of digestive fluids, and subsequent digestion and absorption take place as in *Drosera*.

Pitcher plants. — The *pitcher plants* (*Sarracenia*, *Nepenthes*, etc.), like *Drosera*, commonly are bog plants. The pitcher-like leaf blades of *Sarracenia* (fig. 214) are partly filled with rain water, into which insects, by chance or attracted by the bright colors, frequently wander and are drowned. For crawling insects, entrance is easy and exit difficult by reason of stiff downward-pointing hairs at the edge of the pitcher. In *Nepenthes* nectar is secreted at the pitcher edge, doubtless forming an additional attraction. Proteolytic enzymes have been discovered in the pitchers of *Nepenthes*, the glands occurring at the base of cavities and consisting of spherical multicellular structures, below which are the terminal

tracheids of a conductive bundle, as in *Drosera*. Enzyme secretion probably does not occur in *Sarracenia*, though it is possible that the products of insect decay may enter the plant, much as in saprophytes. In *Dischidia*, an epiphytic pitcher plant, there are double pitchers, one inside the other; the outermost pitcher is a sort of living flower pot in which earth and water collect and into which adventitious roots penetrate from other parts of the plant.

Butterworts and bladderworts. — A third family of carnivorous plants is represented by the butterworts (*Pinguicula*) and the bladderworts (*Utricularia*), which commonly inhabit swamps or ponds. On the leaf blade of *Pinguicula*, as in *Drosera*, there are glandular hairs that secrete viscous substances, and the leaf margins, but not the hairs, also incurve when alighting insects irritate the leaf. The hairs are of two sorts; some with relatively long stalks hold fast to the visiting insects, while shorter hairs, consisting of an eight-celled disk with a hidden stalk, are thought to be more efficient in absorption. The cells secrete enzymes only when the hairs are irritated. The *bladders* of *Utricularia* have an opening at one end, within and about which are a number of hairs and other structures which are so arranged as to prevent egress, though permitting easy entrance, much on the principle of an eel-trap (figs. 215, 216). Minute water animals often crawl or swim into the bladders, where they are detained. The presence of the imprisoned animals has led to a general belief in their utilization by the plant, the forked hairs of the inner surface of the bladder being supposed to play a part in the process, and there is some evidence of the secretion of enzymes and of the digestion of animal food. Bladders may assist in the flotation of the plant, though in such a rôle the eel-trap structures

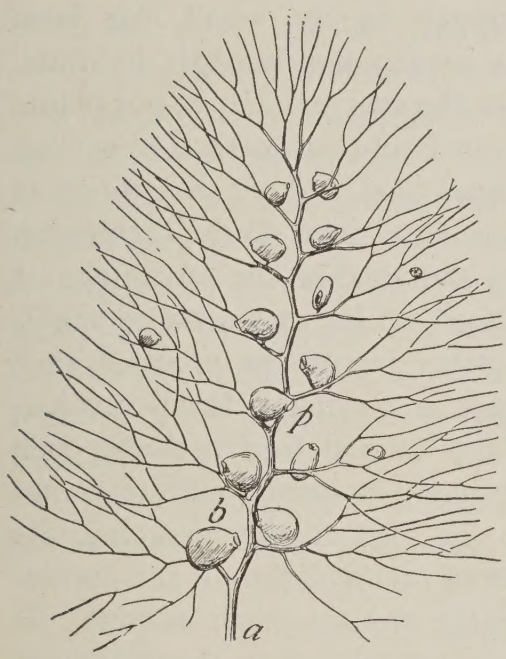


FIG. 215. — A leaf of a bladderwort (*Utricularia vulgaris*), showing numerous capillary divisions, many of which bear bladders (*b*), especially near the place of attachment to the main leaf axis (*a*); note the apertures (*p*) of the bladders into which small aquatic animals may crawl or swim.

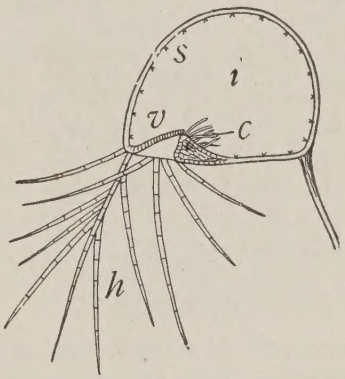


FIG. 216. — A longitudinal section through the bladder of a bladderwort (*Utricularia neglecta*), showing long external hairs (*h*) about the entrance, an elastic valve (*v*) which entering animals readily push back, a cushion (*c*) on which the valve rests, and the interior cavity of the bladder (*i*) in which the animals remain imprisoned; the cavity is lined with small branched hairs (*s*), the so-called absorptive organs of the bladder; considerably magnified. — From KERNER.

can have no significance; it may be noted that bladders occur, though less abundantly, in land species. Possibly the bladders have no rôle of importance. Insects are held by viscid secretions on the stems of *Silene antirrhina* (hence called catchfly), and are drowned in the water-containing leaf cups of *Silphium perfoliatum* and *Dipsacus sylvestris*, but in none of these cases is there evidence of enzyme secretion or of food digestion.

The significance of the carnivorous habit. — The general restriction of carnivorous plants to bogs has led to the view that the carnivorous habit is advantageous in supplementing the nitrogen supply, which has been thought inadequate in such habitats. However, the vast majority of bog plants have no such unusual method of getting nitrogenous food, and yet they thrive as well as or better than do the carnivores. Even in the sundew the advantage of animal food, so far as known, is slight, and in other plants the proof of such advantage is wanting. In all carnivorous plants animal food probably is a comparatively incidental feature of nutrition. In view of the foregoing, the question of the evolution of the carnivorous habit arouses much interest. It has been thought that the glandular hairs of *Drosera* have been derived from water-secreting glands through gradual specialization, but there is no good evidence for this view; even the experimental method of attack is likely to prove unavailing here. The theory of origin through natural selection seems particularly inadequate, partly because in most cases only highly developed organs can be of use, and partly because in all cases the use appears too slight to account for preservation through the operation of natural selection.

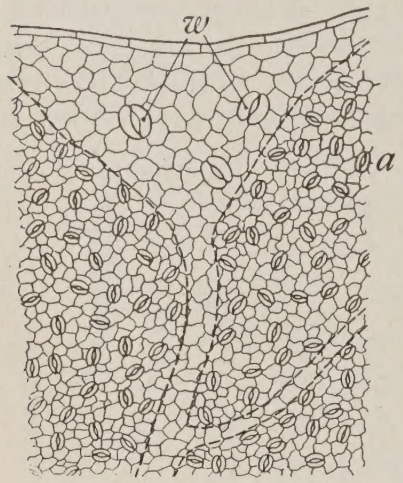


FIG. 217. — A surface view of a nasturtium leaf (*Tropaeolum*), showing large water stomata (*w*) just over the terminal portion of the vein (whose course is indicated by broken lines), and numerous, smaller air stomata (*a*) over the mesophyll region of the leaf; note the irregularity of stomatal orientation, generally characteristic of dicotyl leaves; considerably magnified.

8. LEAVES AS ORGANS OF SECRETION AND EXCRETION

General remarks on secretion and excretion. — *Secretion* usually involves the elaboration of new materials by specialized glands or glandu-

lar regions, whereas *excretion* involves the elimination of waste by any organ. While the products of secretion often play an explicit rôle in subsequent activities, there are many cases in which no such rôle is known, so that it is impossible to regard all secreta as useful and all excreta as useless substances. Plants as a whole have less waste than animals, probably because they utilize simpler raw materials, taking in relatively little useless matter. Plants also differ from animals in that their excreta usually accumulate in reservoirs or in dead or inactive tissues instead of passing off, although excreta are lost in large amount through leaf fall and to some extent through special organs. In any event, the accumulation of waste products in active cells is distinctly disadvantageous, not only because some waste products are toxic, but also because any such accumulations interfere with cell activity.

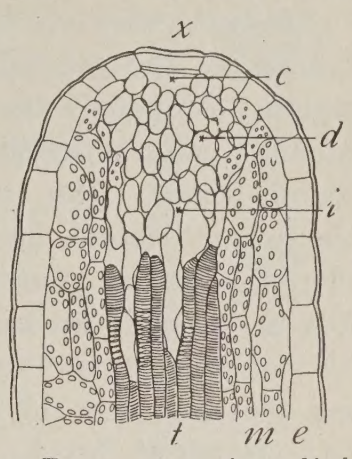


FIG. 218. — A radial longitudinal section through a leaf tooth of the Chinese primrose (*Primula sinensis*), showing a hydathode with divergent tracheids (*t*) terminating the conductive bundle, above which is the colorless epithem (*d*), the stomatal cavity (*c*), and one of the guard cells (*x*) of the water stoma at the tip of the tooth; *i*, intercellular air spaces in the epithem; *e*, epidermis; *m*, chlorenchyma; highly magnified. — From HABERLANDT.

Water exudation. — *Hydathodes.* — When certain plants (as *Tropaeolum*) are placed for some time in a moist chamber, liquid water is exuded from the ends of the principal veins, collecting as drops. The water passes to the exterior through structures, known as *water stomata*, which differ from ordinary air stomata in their position at the ends of veins, in always remaining open, in the lack of the peculiar cutinization characteristic of air stomata, and often by their large size (as in *Tropaeolum*, fig. 217). Underneath the aperture is an air cavity, below which is a loose tissue, the *epithem*, made up of small delicate cells without chlorophyll; underneath this are diverging terminal tracheids, representing the end of a conductive bundle (fig. 218). The entire structure, consisting of tracheids, epithem, and water stoma is called a hydathode (*i.e.* water way). In many plants, as in *Primula*

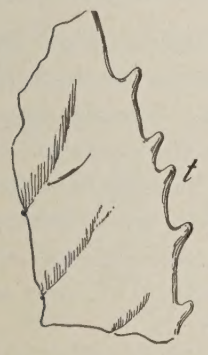


FIG. 219. — A portion of the leaf margin of *Fuchsia*, showing blunt teeth (*t*), each of which represents a hydathode at a vein terminus.

and *Fuchsia*, the hydathodes occur at the tips of bluntish leaf teeth (fig. 219).

The distribution and significance of hydathodes. — Not much is known concerning the general distribution of hydathodes by habitats or regions; commonly they are regarded as most characteristic of the humid tropics, although present in many herbs of low grounds and humid woods. The amount of excreted water may be very large; the tips of *Colocasia* leaves have been known to drip water at the rate of 190 drops per minute, and the leaves of *Conocephalus* are said to lose in one night an amount equal to a fourth of their weight. The substance excreted is nearly pure water, 0.1 per cent or less representing the proportion of salts; closely related to hydathodes are the *chalk glands* of *Saxifraga* and the *salt glands* of *Tamarix*, which excrete, respectively, large quantities of calcium carbonate and sodium chloride. The prevalent theory as to the advantage of hydathodes is that they are a means of escape for a surplus of water in plants with high turgor pressure (" root pressure "), at times when the atmospheric humidity is too great for transpiration. *Water exudation* thereby prevents the injection of air spaces with water and the consequent impairment of respiration and carbohydrate synthesis. There are those who regard the injection of air spaces as an imaginary danger and hydathodes as structures of no evident value; the weight of opinion, however, is for the view first stated.

The mechanics of exudation. — The mechanics of exudation appear relatively simple, water being forced through the influence of turgor pressure along the path of least resistance, namely, through the epithem and water stomata. The phenomenon has much in common with *bleeding*, which may be defined as the exudation of sap from a wounded surface. As with exudation, the amount of bleeding is determined largely by turgor pressure, and it is especially evident when sap is flowing abundantly in spring. Dew and excreted water are likely to be mistaken for one another, particularly as the same atmospheric conditions facilitate both, and as both are likely to appear on leaf teeth.

Various water-excreting organs. — In addition to undoubted hydathodes, organs are found which have been supposed to excrete water. Among such are structures somewhat like those above described, but on submersed leaves (as in *Proserpinaca* and *Ranunculus*); while transpiration is excluded in such plants, there may be an excretion of liquid water, if there is a conductive stream, as sometimes is supposed (p. 124). Water excretion has been thought to be the rôle of epidermal glands which occur close to the terminal tracheids in grooves near the leaf margins of certain ferns. Many hairs (as in *Phaseolus* and *Lathraea*), known as *trichome hydathodes*, have been thought to excrete water through glandular activity. While the exudation of water by these hairs has been doubted, it is easy to believe

in such a rôle because of their close resemblance to nectar glands. Indeed, in the so-called water calyxes of certain tropical plants there are capitate trichome hydathodes that excrete large quantities of water and small amounts of sugar, thus grading into true nectaries. In fungi, water exudation may occur at any point on the plant surface, the entire body frequently being covered with drops of water, especially in caves, mines, and moist chambers.

The influence of external factors upon hydathode development. — Little is known concerning the evolution of hydathodes or of the influence of external factors upon their development. When the hydathodes of *Conocephalus* are poisoned by corrosive sublimate, the air spaces become injected with water, and in a few days hypertrophied tissues are said to protrude from the leaf and excrete water. While these have been called *substitute hydathodes*, and regarded as a sort of emergency adaptation, they are probably nothing more than a case of edema (p. 147), appearing, as usual, where an excess of water is present.

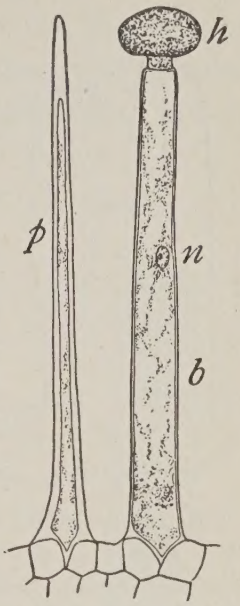


FIG. 220. — Hairs from a vervain leaf (*Verbena stricta*); contrast the pointed, thick-walled, unicellular "protective" hair (*p*) with the capitate, thin-walled, multicellular glandular hair (*b*), the latter being much the richer in protoplasm both in the stalk and in the head (*h*); *n*, nucleus; highly magnified.

The secretion of oils, resins, and mucilage. — *Glandular hairs.* — *Glandular hairs* are distributed widely in plants, and their secretions are often odoriferous (as in *Pelargonium* and in the mints), and usually viscid. Most glandular hairs are multicellular epidermal outgrowths with a head and with a more or less evident stalk; the cells, both in the head and in the stalk, vary in number from one to several and are rich in cytoplasm (figs. 220, 221). In the mints the glandular hairs occur in leaf depressions and are relatively stalkless. In some plants (as in *Silene*) there is a region of palisade-like secretory cells instead of glandular hairs, while in many plants ordinary epidermal cells excrete wax, varnish, etc., as previously noted (p. 85). In oil glands the secretions gather within the walls of the head cells, where they press the cuticle away from the other layers of the wall, ultimately bursting it and discharging to the exterior. The cuticle may or may not regenerate, but in any event old glands lose the power of excretion, the oil accumulating in the cell lumen. Many water plants (as *Brasenia* and

FIG. 221. — A capitate, multicellular glandular hair from a geranium leaf (*Pelargonium*), showing the accumulation of an oil drop (*o*) just beneath the cuticle (*c*); highly magnified.

Nymphaea, fig. 222; also fig. 109) possess *slime glands*, which secrete copiously. In the goldback and silverback ferns (*Gymnogramme*) there is a glandular waxy secretion copious enough to give the leaves their characteristic color.

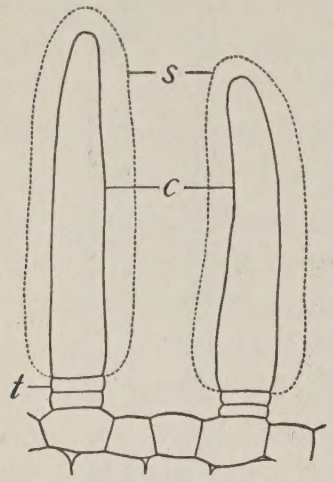


FIG. 222. — Multicellular slime glands of the water shield (*Brasenia schreberi*); note the stalk cells (*t*), the slime-secreting cells (*c*), and the superficial slime layer, whose outer limit is indicated by the dotted line (*s*); highly magnified.

Internal glands. — Many plants possess *internal glands*, which often appear as translucent dots, as in the leaves of *Citrus* and *Eucalyptus*. In most cases the glands are spherical, there being a peripheral layer of glandular cells which secrete into a common central reservoir (fig. 223). Often this structure is surrounded by a relatively impermeable protective layer. Usually the reservoir does not discharge to the exterior, but in *Eucalyptus* and in various Rutaceae there are *cover cells*, which after a time rupture at a definite spot or along the walls, allowing the secretions to pass off. In some cases, as in *Peperomia* and in various liverworts, there are single cells that secrete mucilage (figs. 46, 234). The substances secreted by internal glands resemble those secreted by glandular hairs, and likewise are often odoriferous.

The rôle of oils, resins, and mucilage. — But little is known concerning the rôle of oils, resins, and mucilage, though speculation along this line has been abundant. Wax coats previously have been seen to represent waste products that are of incidental value in protecting against excessive transpiration (p. 86). A similar theory has been proposed concerning excreted volatile oils, on the ground that they absorb heat in large amount, but it is most unlikely that these oils are present in sufficient abundance to check transpiration. Similarly improbable is the common theory that sticky glandular hairs,

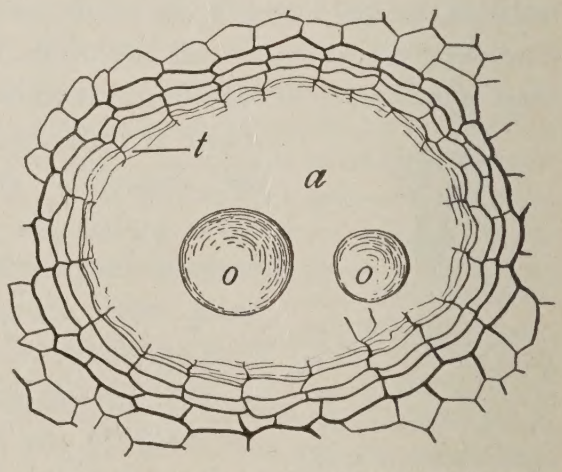


FIG. 223. — An internal oil gland (*a*) in the orange (*Citrus aurantium*); (*o*), oil drops; highly magnified. — From TSCHIRCH.

which are especially abundant on floral stems, are of value in keeping crawling insects away from the flowers, or the theory that various secretions which are unpalatable or even poisonous (as in *Primula*) may lead to the better preservation of plant species from grazing animals. Somewhat more probable but scarcely authenticated are the rôles commonly ascribed to slime in water plants, such as protection from snails and other water herbivores and from water currents. In gelatinous lichens and in amphibious algae, mucilaginous secretions may protect from desiccation. In the economy of aquatic life as a whole, slime plays an important part, since it is a perfect culture medium for many algae, bacteria, and small animals. Probably there is no adequate reason for believing that such secretions as oils, resins, and mucilage are of any particular value in the economy of plants. Doubtless, for the most part, they represent waste products, whose removal is of greater value than their retention. Any incidental gain that these secretions may have probably is small.

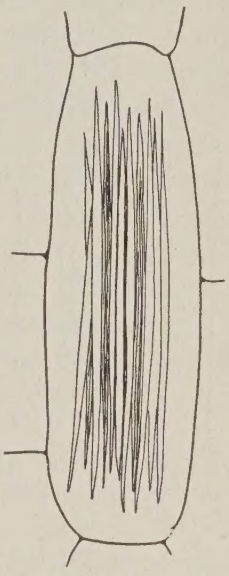


FIG. 224.—A cortical cell from the stem of the wandering Jew (*Zebrina pendula*), showing a group of needle-like crystals (raphides) of calcium oxalate; note the parallelism of the crystals to one another and to the long axis of the containing cell; highly magnified.

The influence of external factors upon gland development and secretion. — Almost nothing is known concerning the influence of external factors upon gland development or secretion. In some cases glandular and " protective " hairs arise from similar primordia (as in *Verbena*, fig. 220), and it has been claimed that the conditions to which such primordia are subjected determine the kind of hair that develops; for example, in *Spiraea*, primordia that are exposed to severe conditions (especially to cold) develop into long, thick-walled protective hairs, while other primordia develop into glands. Similarly, resins and oils are thought to be secreted more abundantly, even in the same species (as in *Rumex acetosella* and in *Primula obconica*), in xerophytic than in other situations. Slime glands are better developed in the water leaves than in the air leaves of *Myriophyllum proserpinacoides*.

Crystals and cystoliths. — *Crystals.* — Calcium oxalate is a very common substance in plants, occurring in the form of needle-shaped crystals (*raphides*, fig. 224), or *crystal aggregates* (fig. 225), or, much more rarely, in the form of isolated crystals with more or less equal axes. Crystals commonly are confined to parenchymatous cells, which often are arranged in longitudinal rows close to the conductive

bundles. Raphides usually are grouped in bundles, the individual crystals being oriented in a common direction; they are particularly abundant in monocotyls with slimy cell sap, while crystal aggregates are perhaps more common in the stems of dicotyls. Crystals sometimes occur in very minute form, constituting the so-called *crystal sand*.

FIG. 225. — A longitudinal section of the cortex of a petiole of the hop tree (*Ptelea trifoliata*), showing longitudinal rows of short cells, each with a compound crystal of calcium oxalate; highly magnified.

Calcium oxalate crystals are undoubted excreta, representing by-products of metabolism. Oxalic acid in the free state, existing as a solute in the cell sap, is believed to be poisonous, especially if present in large amount, though in the various sorrels it is abundant enough to give them their characteristic taste. Even if not poisonous, free oxalic acid certainly is deleterious, since its formation interferes with further cell activity, as does sugar or any other product of metabolism, unless transformed into an insoluble substance or removed to other cells. Thus the chief advantage of crystals is in removing oxalic acid from solution. Sometimes it is held that crystals are beneficial in removing calcium from solution, especially in calcareous soils, though this view has not met with general acceptance. It has been held also that raphides by their sharp points protect plants from injury by snails, but the evidence for this theory is negative. Still more untenable are the theories that crystals give mechanical support to plants and that they represent accumulations of calcium that later may be utilized. In most cases it is not necessary or even desirable to seek a subsidiary function for the excreted products of plants; if in certain instances they have such a function, it must be regarded as wholly incidental.

FIG. 226. — A spindle-shaped cystolith with warty protuberances from the leaf of *Pellionia;* highly magnified.

Cystoliths. — In various Urticales there occur aggregates of calcium carbonate, known as *cystoliths*, whose rounded rather than angular projections readily distinguish them from crystals. In *Pilea* and *Pellionia* they are spindle-shaped and lie free in the cell (fig. 226), while in *Ficus* they are stalked and mulberry-shaped. When treated with acid, the rounded knobs effervesce, leaving an insoluble, stratified cellulose skeleton. While the rôle of cystoliths is unknown, it is

probable that as waste products they may serve to remove from solution an excess of calcium salts, though some regard them as calcium accumulations that subsequently may be used. Some plants contain warty siliceous bodies somewhat resembling cystoliths.

Various products of secretion and excretion. — Various products, mainly excretions, accumulate more in stems than in leaves, and will be considered elsewhere (p. 233). The sharp taste of mustards, capers, and nasturtiums is due to an oil, formed by the action of a ferment, myrosin, upon calcium myronate. Many plants contain *alkaloids*, most of which are violent poisons, as *strychnin*, *atropin*, and *cocain*. Bitter principles are illustrated by the *absinthin* of wormwood and the *aloin* of aloes, and poisonous glucosides are represented by *digitalin* and *solanine*. Such substances as a class probably are by-products of metabolism, and if, as suggested, they protect against animals, either because poisonous or unpalatable, such protection is purely incidental. Even this incidental use is likely to be overestimated, since plants that are poisonous or disagreeable to man are not necessarily so to all herbivorous animals. Furthermore, the organs most likely to be eaten, the leaves, usually contain poisons and unpalatable substances in less amount than do the other organs.

9. LEAVES AS ORGANS OF ACCUMULATION OF WATER AND FOOD

Food accumulation in leaves. — Generally it would be disadvantageous for leaves to serve as organs of food accumulation or " storage," since this would impair their synthetic efficiency, partly because of the space that such foods would occupy, and partly (in the case of soluble foods, like the sugars) because increasing concentration retards further manufacture. Leaves serve as organs of temporary accumulation, because in the daytime, foods usually are manufactured faster than they are removed to other organs; during the night, however, removal continues, so that the leaf is relatively free from accumulated foods by morning. In various desert xerophytes in which the leaves remain for years, large quantities of food and water may accumulate, as in *Agave*, whose developing flower-stalk so drains the leaves of their contents that they fall back limp and wrinkled (figs. 227, 228).

General features of water-accumulating leaves. — *Water retention.* — In leaves the accumulation and retention of water in conspicuous amount is much more common than that of foods, and is especially characteristic of *succulent* xerophytes, such as the Crassulaceae and Chenopodiaceae. The water retentiveness of such plants is well shown when attempts are made to dry them; Crassulaceae and Cactaceae frequently grow for days or even for weeks while being dried under pressure for herbarium specimens. This retentiveness is due

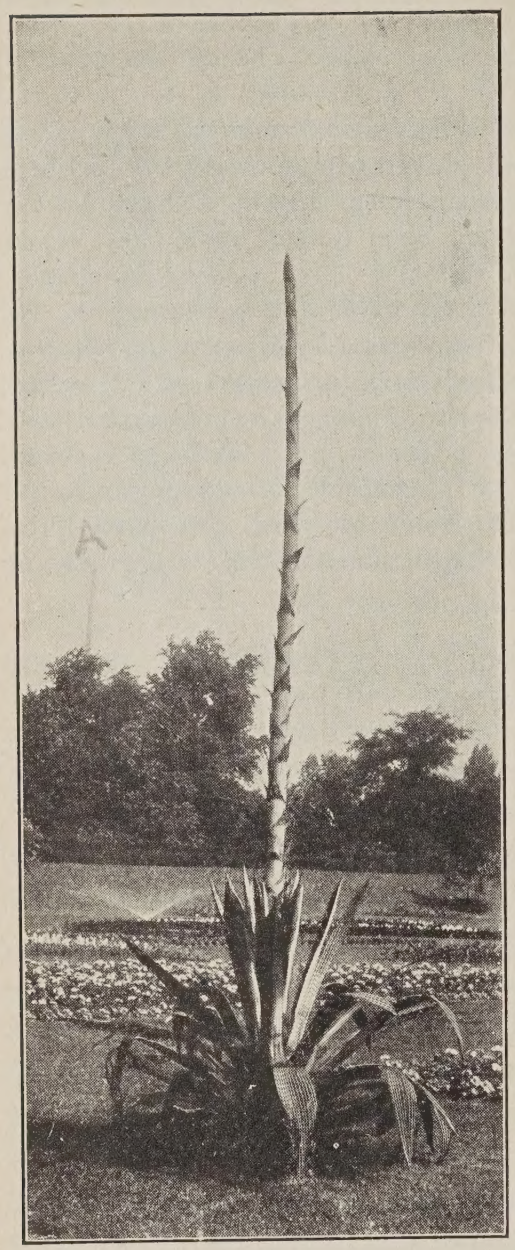


FIG. 227

FIG. 228

FIG. 227. — The century plant (*Agave americana*) at the time of the rapid development of its gigantic inflorescence; note the growing flower-stalk with its large bracts and the rosette of stiff foliage leaves; Washington Park, Chicago, Ill. — Photograph by FULLER.

FIG. 228. — The century plant (*Agave americana*), showing a fully developed inflorescence; note that the leaves, deprived of their accumulated water and food by the growing inflorescence, have fallen back limp; the plant dies after the ripening of the fruit; Washington Park, Chicago, Ill. (the same plant as in Fig. 227, two months later). — Photograph by FULLER.

in some instances to high cutinization (Cactaceae), or to waxy coats (Crassulaceae), or to both combined (*Agave*); most succulent plants, however, exhibit weak cutinization. Another character favoring retentiveness in succulent leaves is a small evaporating surface in proportion to the volume, but many orchid leaves which evaporate slowly are thin and slightly cutinized (as in species of *Habenaria*). Again, in many succulents which have a cell sap of high osmotic pressure, evaporation doubtless is relatively slow. The best attested cases of such concentrated cell sap are in the succulent plants of salt marshes, which may have an osmotic pressure equal to 40 to 50 atmospheres, and in various desert plants, largely shrubs, some of which may have a pressure of more than 100 atmospheres, as compared with a pressure of 5 to 20 atmospheres in plants of ordinary habitats. The osmotic pressure in cacti, on the other hand, has been shown to approximate that in ordinary plants. Probably upon this basis succulent plants may be divided into two classes: (1) salt marsh and other succulents (which include the most representative forms) having sap of high osmotic pressure, and (2) succulents whose water retentiveness is due to structural or other characters, notably cutinization, as in the cacti. It is probable, however, that no explanation thus far given accounts for all cases of extreme water retention in the presence of conditions favoring transpiration.

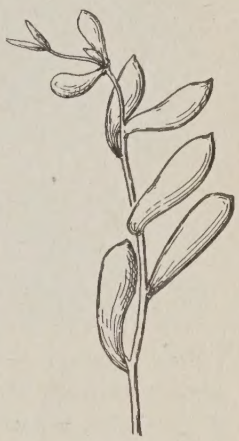
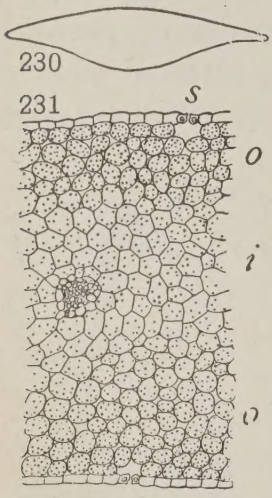


FIG. 229. — A branch of *Senecio* sp., a desert xerophyte, illustrating extreme leaf succulence, the very fleshy leaves presenting a small surface in proportion to their volume.

Structural features. — While most leaves are *dorsiventral* (*i.e.* with the upper and under portions different in structure), many succulent leaves are cylindrical and almost *radially symmetrical*, like stems and roots, instead of having only one plane of symmetry, as do most leaves (fig. 229).[1] However, while the epidermis, chlorenchyma, and colorless parenchyma, as seen in cross section, are essentially uniform in aspect in the entire leaf cylinder, the conductive tract is dorsiventral, as in ordinary leaves, the xylem being above and the phloem beneath (fig. 232). In succulent leaves the veins commonly are buried so deeply as to be inconspicuous from without.

[1] Most dorsiventral leaves present two distinct surfaces and hence may be called *bifacial*, contrasting with cylindrical *equilateral* leaves.

Water tissue. — All the living plant tissues are composed chiefly of water, but the term *water tissue* is employed especially in succulent plants to designate regions of turgescent parenchyma cells with delicate cellulose walls, thin peripheral layers of cytoplasm, and few or no chloroplasts. In many succulents the water tissue is not sharply delimited from ordinary chlorenchyma, and may be made up entirely of turgescent green cells (as in various thin-leaved succulents), quite as in most leaves except for the evident fleshiness of the organ; or the leaf may be thick with the chlorophyll gradually decreasing toward the center, the cells otherwise being essentially similar in aspect, as in most Crassulaceae (figs. 230, 231); or the leaf may be thick with chlorophyll decreasing toward the center, but with the outermost chlorenchyma cells elongated, representing true palisade



FIGS. 230, 231. — Cross sections through the leaf of *Cotyledon*, a succulent xerophyte: 230, a diagrammatic section, showing that the leaf is relatively thick in proportion to its width; 231, a cross section, considerably magnified, showing relatively uniform chlorenchyma cells, except that the outermost cells (*o*) are rounded and the innermost cells (*i*) angular; note that stomata (*s*) occur on both surfaces and that chlorophyll and air spaces are more abundant in the outermost than in the innermost cells.

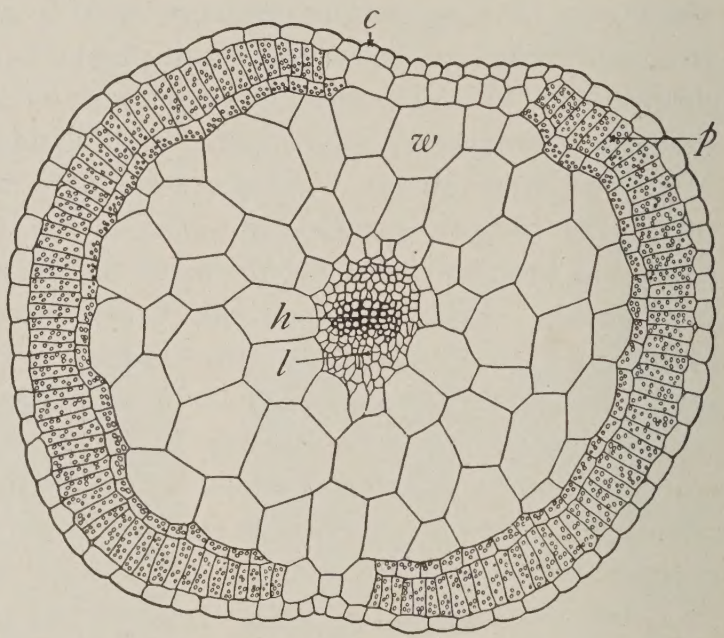


FIG. 232. — A cross section through a succulent xerophytic leaf, that of the Russian thistle (*Salsola kali tenuifolia*), illustrating peripheral palisade chlorenchyma (*p*) and central water tissue (*w*); note the relatively thin cuticle (*c*), and the sharp delimitation between the chlorenchyma and the water tissue, the latter being characterized by the large size of the cells and by the absence of conspicuous air spaces; such a leaf is equilateral and approximately radially symmetrical, thus having a small surface exposure in proportion to the leaf volume; dorsiventrality is exhibited alone by the vascular bundle, the hadrome or xylem (*h*) lying above the leptome or phloem (*l*); highly magnified.

cells, while the cells toward the center become more and more isodiametric and also poorer in chlorophyll (as in the century plant and in various cacti). Another kind of water tissue characterizes more extreme succulents (as *Salsola* and other forms with cylindrical leaves) and may be regarded as more representative; in these plants the water tissue, which is composed of large isodiametric cells, is centrally placed and is more or less sharply delimited from the peripheral chlorenchyma cylinder whose cells usually are relatively small and of palisade shape (figs. 232, 233).

A third kind of water tissue differs from all the rest in its peripheral position, the cells belonging to the epidermis rather than to the mesophyll. All gradations occur between an ordinary epidermis with a single layer of colorless water-containing cells and a many-layered epidermis of similar but more turgescent cells, as in *Begonia* and *Peperomia*, where the centrally placed chlorenchyma occupies less space than does the epidermal *water mantle* (figs. 234, 67, 68). Perhaps the commonest sort of water mantle is represented in *Tradescantia*, where there is a single or double layer of large turgescent colorless cells. The water tissue commonly is best developed on the upper side of the leaf, sometimes being confined to that side. In most cases the cell sap is highly acid.

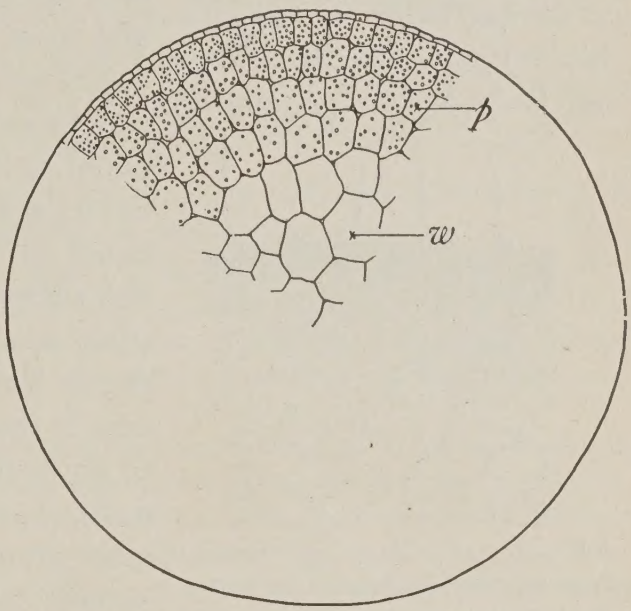


FIG. 233. — A sector from a cross section of a succulent equilateral xerophytic leaf (*Senecio* sp.), illustrating peripheral palisade chlorenchyma and central water tissue, but showing a gradual transition from the former to the latter, both in cell size and in chlorophyll abundance; lettering as in Fig. 232; considerably magnified.

In the " ice plant " (*Mesembryanthemum crystallinum*) a few of the epidermal cells are much distended and project considerably beyond the epidermal level, causing the leaves to glisten in the sunlight. Not infrequently plants possess isolated colorless turgescent cells in the midst of a tissue made up of cells of wholly different character; when such cells have walls with tracheid-like thickenings, they have been called *storage tracheids* (fig. 73). In many succulent monocotyls (as *Aloe*) the

cell sap is very mucilaginous, and in some plants of similar character mucilaginous material is deposited in the form of wall thickenings.

The causes of water accumulation in succulent plants. — *Experimental data.* — Some succulent plants (e.g. *Sempervivum assimile*, figs. 350–352) when placed for a few weeks in a moist chamber develop slender elongated shoots with thin expanded leaves, having little or no suggestion of succulence, while subsequent removal to dry air results once more in the development of short and stout shoots that bear thick succulent leaves of small size. Such reactions are quite like those previously noted as characterizing habitats that differ in atmospheric humidity and hence in transpiration (see p. 113). But while the xeromorphic leaf is in all cases small and thick and the mesophytic leaf large and thin, the thickness in the succulent xerophyte is due to an increased dorsiventral development of watery tissue, while that in other xerophytes (as *Ledum* or *Campanula*, figs. 173, 174) is due to increased cutinization and to palisade development. Apparently these different xeromorphic reactions are due to similar causes, namely, either a deficient water supply or exposure to increased transpiration.

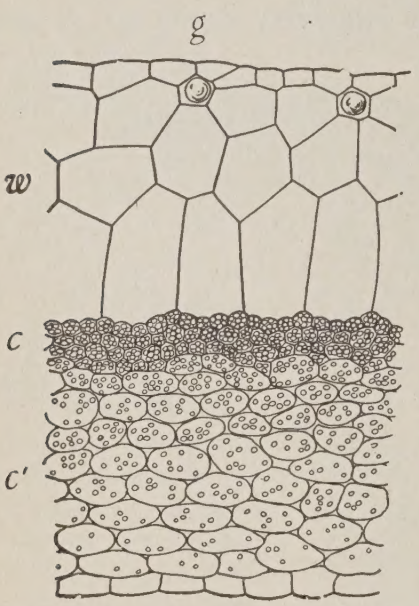


FIG. 234. — A cross section through a *Peperomia* leaf, illustrating peripheral or epidermal water tissue (*w*), the epidermis being three or four layers thick and containing mucilage glands (*g*); note that the uppermost chlorenchyma layers (*c*) consist of small closely packed cells with abundant chlorophyll, while the lowermost chlorenchyma layers consist of larger and more loosely placed cells with less chlorophyll; highly magnified.

Not only does the reference of succulence to transpiration bring it into line with other xerophytic characters, such as cutinization and palisade development, but like these, succulence develops in analogous situations, as in maritime habitats. Years ago it was shown that *Salicornia*, one of the most succulent of halophytes, loses much of its succulence when grown where the soil is poor in sodium chloride, while its succulence increases with the addition of this salt to the soil. The same is true of *Glaux maritima*, *Rhizophora*, and various other salt plants. The dorsiventral leaves of the beach pea and the wallflower

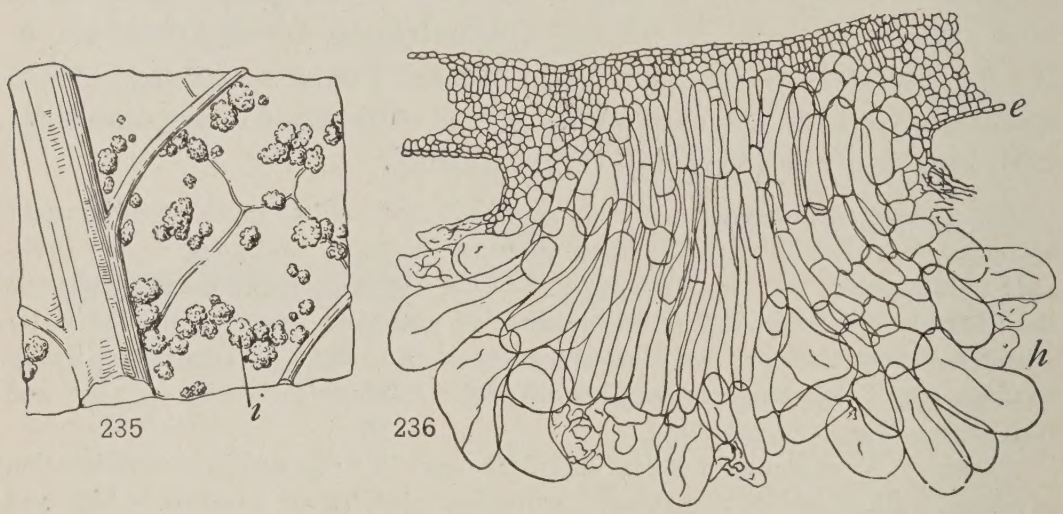
tend toward equilaterality in salty soils, precisely as they do when exposed to strong transpiration. Similarly, plants of alkali deserts (as *Halimodendron*) show a reduced development of water tissue when grown in ordinary garden soil. In so far as succulence involves increased cell turgidity and sphericity, the influence of transpiration or of salt solutions of high osmotic pressure is essentially the same as in *Stigeoclonium*, where these characteristics accompany high concentration of the cell sap, however produced (p. 106). Usually a desert plant is exposed to high transpiration, and often absorption is slight; such conditions result in cell-sap concentration, which favors succulence. Similarly, a *Salicornia* plant in a salt marsh is exposed to transpiration, while at the same time the soil salts make absorption difficult, also resulting in cell-sap concentration.

The problem of water accumulation may have to do not so much with increased water accumulation as with the distribution of the water-containing cells. Probably a leaf appears succulent, less because of the large amount of water it contains than because its thickening at the expense of expansion concentrates the water within a compact region; and leaf compactness in contrast to expansion already has been seen to be connected largely with high relative transpiration (p. 113), and thus with cell-sap concentration.

Edema. — An explanation of leaf succulence may be suggested by a consideration of *edema*, a phenomenon occasionally witnessed when turgor pressure is high and transpiration low, and evidenced externally by the appearance over the leaf surface of whitish emergences, known as *intumescences* (figs. 235, 236). Intumescences develop on the leaves of *Hibiscus vitifolius*, *Solanum tuberosum*, and various other plants in moist chambers, and also on isolated leaves of *Populus* and *Eucalyptus* and on the inner surfaces of pea pods that are placed in water; in the tomato they have been induced by forcing water into cut stems and by heating the soil in which they grow. In all these cases a surplus of water in the plant causes the hypertrophy of the leaf tissues, which, for lack of space within, are forced to break through the epidermis as intumescences. Probably " water lenticels " (p. 179), the " substitute hydathodes " of *Conocephalus* (p. 137), and the " breathing roots " of *Jussiaea* (p. 25) are essentially identical with intumescences, not only having a similar aspect but also developing under similar conditions. In some cases intumescences are developed also by chemical stimulation, as in the leaves of the cauliflower (figs. 235, 236).

Succulence and intumescence. — While succulent and intumescent leaves seem to have certain superficial resemblances, each being very juicy and having cells filled almost to bursting with cell sap, they differ in most essential respects. Intumescence clearly is associated with a relative surplus of water, while succulence commonly is associated with a relative surplus of salts. The best conditions for active growth border closely on those which induce intumescence, water being present in sufficient amount to make the cell sap dilute and thus permit unrestricted cell activity. Indeed, the phenomena of edema mean that growth within the leaf is so

rapid that expansion fails to keep pace with it. Succulence, on the other hand, results from sluggish growth, the water, because of its large percentage of solutes, being utilized less freely. When exposed to transpiration, the intumescent plant withers quickly, while the succulent plant long retains its moisture, owing to the large amount of solutes. However, not all cases of leaf succulence are to be explained thus. In some cases the cell sap is known to be dilute, and in many instances its condition is yet to be investigated. Still less is known as to the factors involved in the origin of concentrated cell sap, except, perhaps, in halophytes. It has been suggested that the respiration of succulent plants is imperfect, thus leading to the accumulation of osmotically active substances which facilitate further succulence;



FIGS. 235, 236. — Intumescences produced on cauliflower leaves (*Brassica oleracea*) by chemical stimulation, the leaves having been sprayed with copper ammonium carbonate; 235, a small portion of the lower leaf surface, five days after spraying; *i*, intumescences: 236, a cross section through an intumescence, highly magnified; note the greatly hypertrophied mesophyll cells (*h*), which have broken through the lower epidermis (*e*). — From VON SCHRENK (235 drawn from a photographic reproduction).

it is difficult, however, to understand the inception of such a process. Still more inexplicable is succulence in such plants as *Begonia* and *Peperomia*, which have fleshy leaves in the humid atmosphere of the rain forest.

The advantages of succulence. — *General advantages.* — Even though a succulent plant is unwatered for a long time, the growing parts show no cessation of activity, new shoots continuing to develop by utilizing the water in the older organs. The old leaves shrink and become wrinkled, the cells collapsing to a greater or less degree. The functional significance of leaf succulence is to be found chiefly in the protection of the synthetic tissue. Leaves are in general ill-fitted for water retention, since they are much more subject to excessive transpiration than are stems and roots. Furthermore, leaf succulence must impair synthetic activity, partly because of the weakening of incident

light in traversing the leaf, and partly because the accumulation of solutes impairs sugar formation and other cell activities. However, in extreme xerophytes it is not a question between ample and slight synthetic activity, but between slight activity and none at all; the very presence of abundant water and solutes, though tending generally to reduce synthesis, may here be the means of permitting synthesis through the protection thus afforded to the chlorenchyma. Such protection may vary with the relative arrangement of the water tissue and the chlorenchyma. Whether its position is peripheral or central, water passes from the water tissue to the chlorenchyma, whenever the supply in the latter becomes scanty, thus permitting the continuance of synthetic activity. Peripheral water tissues also may tone down the intensity of the incident light, thus permitting synthesis to continue even in bright sunlight. It has been shown experimentally that a leaf with a surface layer of water becomes less heated on exposure to light than does the same leaf without such a layer.

Peripheral water tissues. — Peripheral water tissues commonly are associated with expanded dorsiventral leaves and are especially characteristic of the tropical rain forest, where they are found particularly in epiphytes (such as the orchids and bromelias), whose water supply is more limited than that of the trees on which they grow, because they can absorb water only when it is in contact in liquid form with their aerial organs; similar tissues occur also in the leaves of various trees, as in *Ficus*, and even in those of such mesophytes as the banana. Except in the epiphytes, the advantage of water tissue in the rain forest is not obvious, though it has been suggested that the water mantle is of value, even there, as a means of reducing the intensity of the light and of lessening the occasionally high transpiration. In the case of *Begonia* and *Peperomia*, plants with pronounced leaf succulence that often live in the dense shade of the forest bottom, it has been shown that the conducting capacity of the stems is limited and hence the succulence may be of survival value during brief intervals of high transpiration due to exposure to direct sunlight. That in *Begonia* some species, at least, are essentially, rather than apparently, xerophytic is shown by their frequent cultivation in houses in relatively xerophytic conditions, while most of their associates of the rain forest (such as the filmy ferns) require the most humid of conditions for successful cultivation. It is difficult to imagine any advantage in succulent leaves in the depths of the rain forest.

The significance of succulence in extreme habitats. — In the most extreme desert xerophytes and in the plants of salt marshes and alkali regions, equilateral leaves with centrally placed water tissue are very characteristic. There is little doubt that succulence represents the culmination of xerophytic characters and that the equilateral leaf with central water tissue represents the most xerophytic of leaf

forms. Salt deserts are the most unfavorable of habitats, since with the most excessive transpiration there are combined the poorest conditions for absorption, by reason of the high concentration of the soil solutions. Among the higher plants the forms which penetrate the farthest into these barren regions are the succulents. In conditions where existence is impossible for the sagebrush with its hairy leaves, or for the creosote bush with its varnished leaves, or even for the leafless cacti with their great quantities of accumulated water protected by cutin, there flourish various Chenopodiaceae (such as *Salsola*, *Sarcobatus*, or *Suaeda*) with their fleshy equilateral leaves. Three features appear to be responsible for the remarkable endurance of such leaves: the small evaporating surface, which is the least of any leaves; the large amount of water, which serves to tide over long unfavorable periods; and, finally, the high concentration of the cell sap, which makes water retention possible in spite of prolonged exposure to conditions that cause desiccation in plants with dilute cell sap.

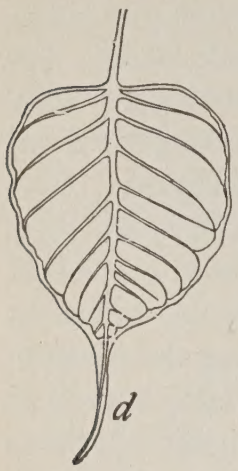


FIG. 237. — A leaf of *Ficus religiosa*, a tree of the tropical rain forest, showing a so-called dripping point (*d*). — After STAHL.

10. MISCELLANEOUS LEAF STRUCTURES AND RELATIONS

Leaves as organs of run-off. — As previously noted, hairy coats and surface excretions often are of value, especially in water plants, in preventing the wetting of leaf surfaces, thus facilitating an undisturbed exchange of gases through the stomata. In the rainy tropics, where storms occur daily and where the air is almost constantly humid, many leaves have long attenuated tips, sometimes known as *dripping points* or *gutter points*, which are supposed to facilitate the run-off of precipitated water that might otherwise impede stomatal activity (fig. 237). Grooved and channeled petioles may act similarly. It has been

FIG. 238. — A portion of a leaf of a tropical *Asplenium*, illustrating reproduction by leaves; on the under sides of the ultimate leaf divisions (pinnules) are fruit dots or sori (*s*), in which are sporangia with their spores; on the upper sides of the pinnules are bulbils (*b*), which here have germinated while connected with the parent plant, giving rise to bulblings whose leaves (*l*) already are conspicuous.

suggested that there is a sort of correlation between run-off and root direction, horizontal roots characterizing plants with leaf drip, and vertical roots those with petiole drip; while this is unlikely, the direction of root growth might be thus determined if run-off were the sole source of water, since roots are prohydrotropic.

Leaves as reproductive organs. — *Ferns.* — In the ferns the foliage leaves commonly bear sporangia, which are grouped in brownish fruit dots (*sori*) on the back of the leaf (as in *Aspidium*, figs. 434, 435), or are borne under the recurved leaf

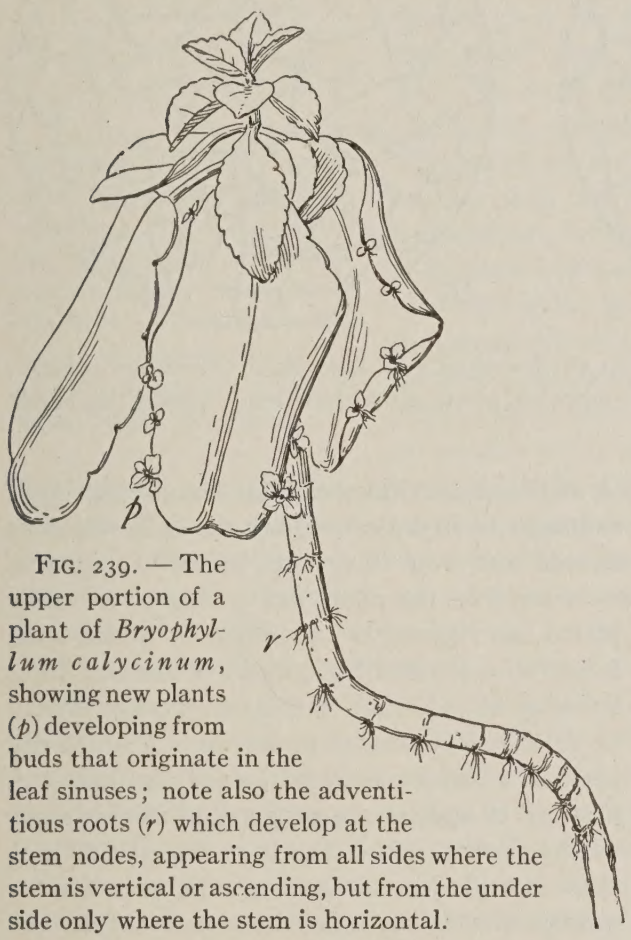


FIG. 239. — The upper portion of a plant of *Bryophyllum calycinum*, showing new plants (*p*) developing from buds that originate in the leaf sinuses; note also the adventitious roots (*r*) which develop at the stem nodes, appearing from all sides where the stem is vertical or ascending, but from the under side only where the stem is horizontal.

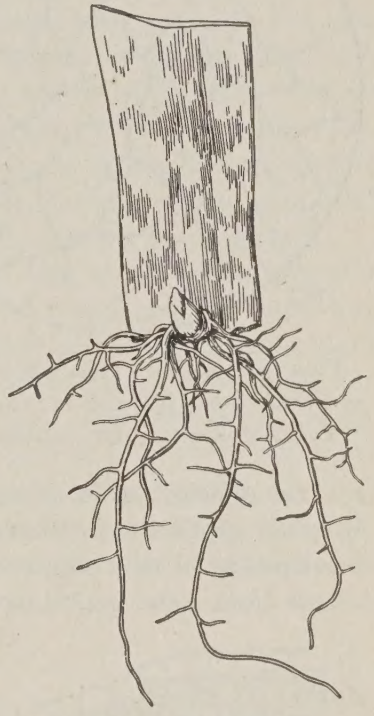
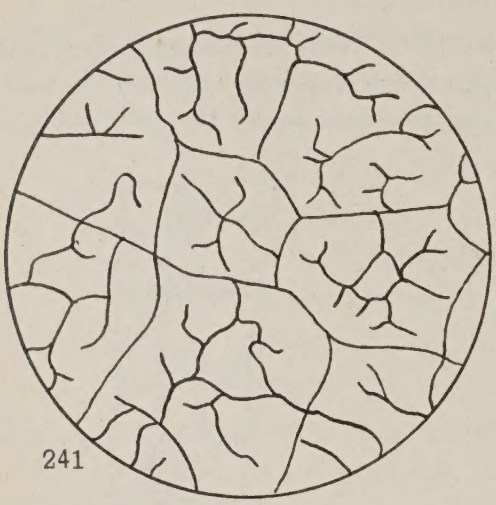


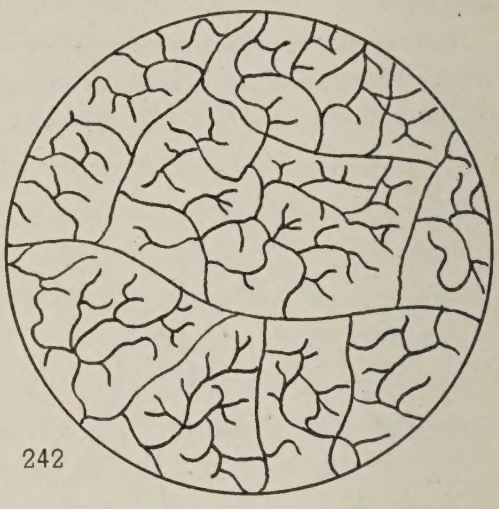
FIG. 240. — Vegetative reproduction in *Sansevieria* artificially induced through the use of a leaf cutting; a bud and a copious growth of roots originate at the basal part of the cutting when placed in moist soil.

margins (as in *Pteris*). In some ferns (as *Osmunda*) the sporangia are borne on special reproductive branches, or even on special leaves which contrast strongly with the foliage leaves. Fern leaves may take part also in vegetative reproduction. *Cystopteris bulbifera* and species of *Asplenium* develop leaf *bulbils*, which in *Cystopteris* drop off and germinate in the ground. In *Asplenium* they may germinate and grow to considerable size while attached to the leaf (fig. 238), later falling to the ground where development is continued. When the leaf tip of the walking fern (*Camptosorus*) comes in contact with the ground, a bud forms from the terminal cells, later developing into a plant. In *Adiantum edgeworthii* the apical cell of a leaf may develop directly into a stem. In *Camptosorus* some external factor (perhaps moisture) stimulates vegetative reproduction, but the stimulating factor in

Asplenium and *Cystopteris* is unknown. The leaves as well as various other organs of mosses exhibit vegetative reproduction (see p. 322).

Seed plants. — In the seed plants natural leaf reproduction is a rare phenomenon. In *Tolmiea* and in *Cardamine pratensis* new plants may appear on the leaf blade





FIGS. 241, 242. — The finer veins in the leaves of a tobacco plant (*Nicotiana rustica*); 241 from a lower leaf and 242 from an upper leaf on the same erect stem; equally magnified. — From Maximov after ZALENSKI.

near the petiole, and in *Bryophyllum* at the sinuses along the leaf margin (fig. 239). Moisture appears to facilitate development in *Bryophyllum*, but the more vigorous development of new plants on a severed leaf, even in dry air, seems to suggest a release from some inhibitory factor residing in the plant (see p. 264). In many plants (as *Peperomia* and *Begonia*) a bud soon forms on a severed leaf placed in the soil, later growing into a plant; in *Sansevieria*, leaves may be cut into a number of pieces, each of which will produce a bud if placed in the soil (fig. 240). A number of species are propagated in this manner by florists, and it has been shown that as a class dicotyls have a much greater capacity for propagation by leaves than have monocotyls. In a great many species whose leaves appear unable to give rise to new plants, roots originate somewhat readily from the leaves. These plants rarely exhibit leaf propagation in nature, chiefly because living leaves rarely fall to the ground. Hence in seed plants the capacity for leaf propagation is not especially advantageous.

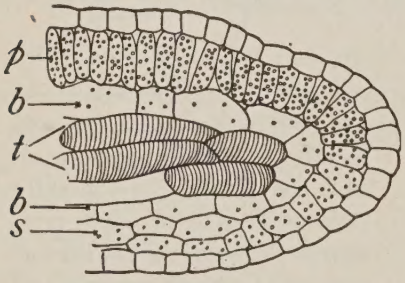


FIG. 243. — A longitudinal radial section of a leaf of the hop tree (*Ptelea trifoliata*) near the end of a vein, showing a bundle terminus with its tracheids (*t*), surrounded by a bundle sheath (*b*); note that the upper chlorenchyma consists of palisade cells (*p*), which at the leaf margin grade into the cells characterizing the lower chlorenchyma (*s*); highly magnified.

Conductive tissues in leaves. — *General features.* — *Veins* are the mechanical framework of leaves and also the paths of conduction, and differences in *venation* form most conspicuous leaf features. Most dicotyl leaves have a prominent *midrib*, whose branches fork and anastomose repeatedly, thus forming

a reticulated network of small veins (fig. 241). The midrib and the larger veins are the main trunk lines along which water and foods pass, and the smaller veins connect these with the chlorenchyma. In some dicotyls (as in the maples, fig. 82) there are several *primary veins*, while most monocotyls have several to many equal and more or less parallel primary veins, connected by rather obscure transverse veins. It has been shown that under conditions of deficient water supply or of exposure to unusually high rates of transpiration there are developed more veins per unit area than under more mesophytic conditions (figs. 241, 242). In most conifers and in many narrow-leaved angiosperms there is a midrib with few or no branches. Veins often are inconspicuous in succulent xerophytes because they are deeply buried, and in submersed hydrophytes, because they are poorly developed.

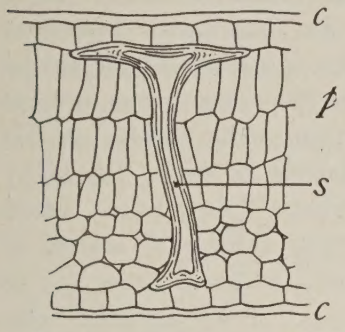


FIG. 244. — A cross section through a leaf of the fragrant olive (*Osmanthus fragrans*), showing a T-shaped sclereid (*s*), which together with the thick cuticle (*c*) accounts for the stiffness of the leaf; note the three palisade layers (*p*), indicating relative xerophytism; highly magnified.

Structural features. — Leaf veins, like conductive tracts generally (p. 198), are composed of water-conducting elements (*hadrome*), food-conducting elements (*leptome*), mechanical elements (*stereome*), and undifferentiated parenchyma. The position of the hadrome cells in the upper portion of the vein just above the leptome (fig. 61) and near the palisade cells may be advantageous, since the amount of water transported greatly exceeds the combined amount of other substances. Near the ends of the veinlets there are no tracheae, but chiefly tracheids which frequently diverge in such a way as to increase the area of the diffusing surface (fig. 243); commonly they are surrounded by a sheath of mesophyll cells.

Mechanical tissues in leaves. — Mechanical leaf tissues, while mostly lacking in hydrophytes and not especially well developed in mesophytes, are developed prominently in many xerophytes, particularly in those with stiff evergreen leaves, the so-called *sclerophylls*. As noted elsewhere, the cutinized outer epidermal wall is an important means of stiffening in these and other leaves, supplemented in some cases by a thickening of the lateral epidermal walls (as in *Ficus*, fig. 104) or even of the hypodermal walls (as in *Pinus*, fig. 346). In the leaves of xerophytic grasses and sedges, patches of thick-walled bast fibers and other mechanical cells may occur just beneath the epidermis (fig. 141), and festoons of such cells often surround the conductive bundles, giving a great amount of strength to the leaves. Sometimes (as in *Osmanthus*, fig. 244) evergreen leaves contain isolated mechanical cells (*sclereids*) extending from the lower to the upper epidermis, apparently acting as supports or braces; occasionally these stiff cells are Y- or

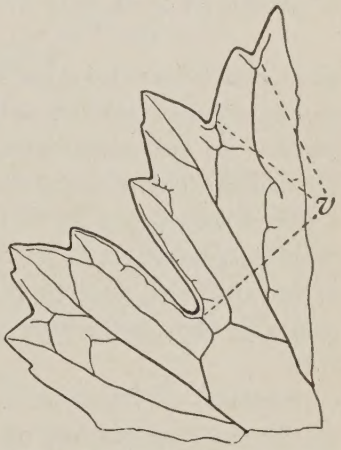


FIG. 245. — A portion of a leaf of the golden currant (*Ribes aureum*), showing arcuate veins (*v*) just below the leaf sinuses, where the danger of tearing otherwise would be considerable.

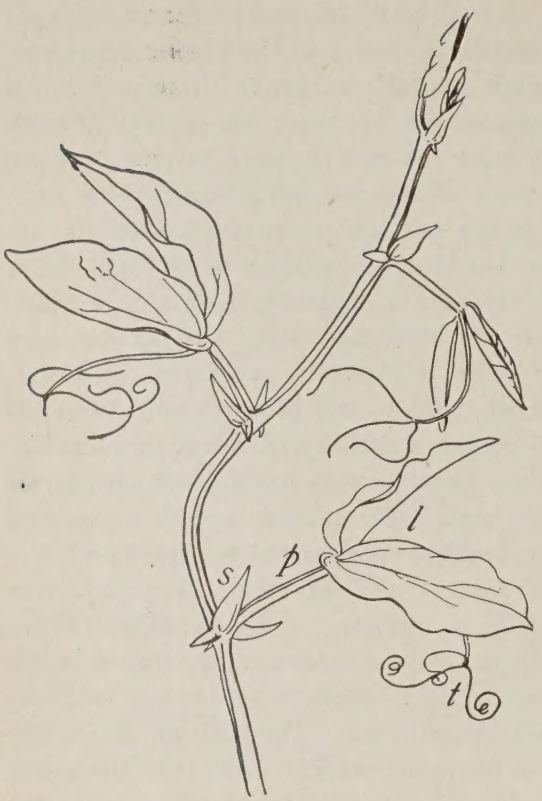
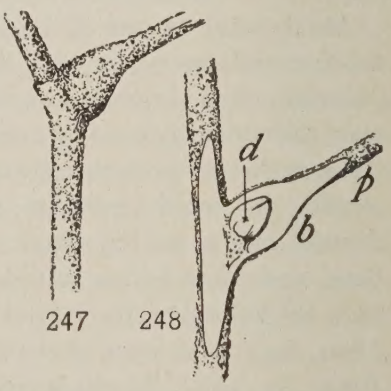


FIG. 246. — A growing shoot of the sweet pea (*Lathryus odoratus*), showing leaves with a pair of leaflets (*l*), a terminal tendril (*t*), and a pair of stipules (*s*) at the base of the petiole (*p*).

T-shaped. The outer layers of most petioles have the collenchymatic thickening characteristic of young stems (p. 212). The tearing of leaves at their margins is prevented largely by the presence there of an extra amount of cutinization, while similar protection is afforded in many leaves by marginal veins. Lobed leaves would seem especially subject to tearing at their sinuses; in some cases (as in *Ribes*, fig. 245) strong arcuate veins just beneath the sinus prevent such tearing. Sometimes such marginal protecting structures are wanting, as in the banana leaf, which consequently is shredded by the winds (fig. 152).

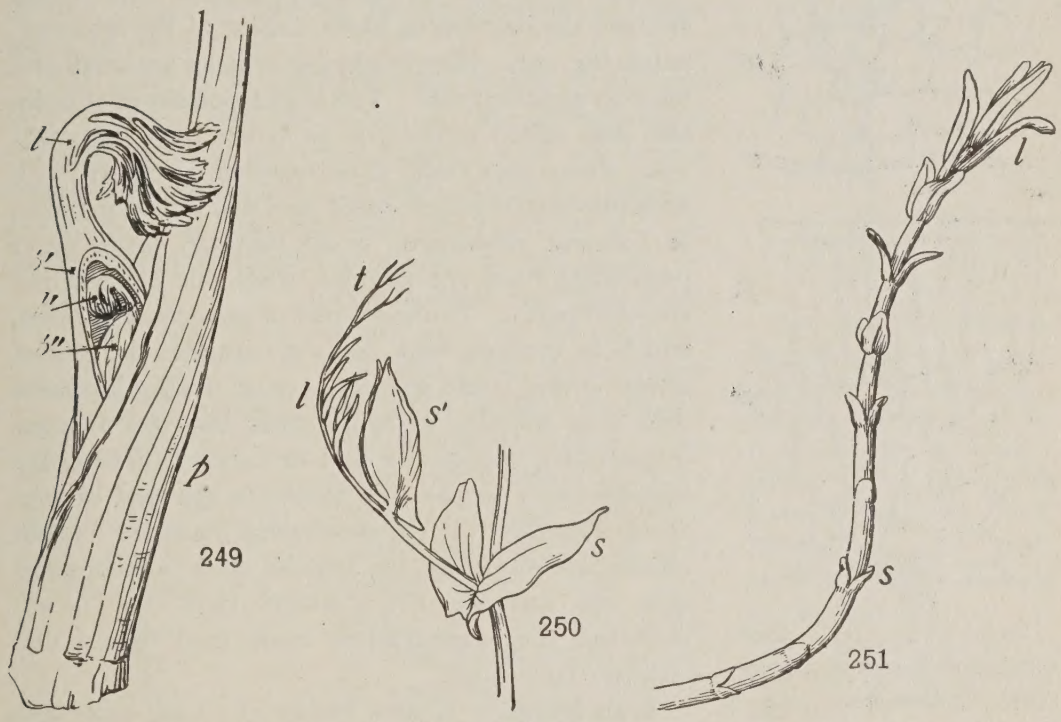
Leaf tendrils. — Climbing organs in general will be considered under stems (p. 168), but some plants (as vetches and peas, figs. 246, 250) climb by means of leaf organs, the upper leaflets consisting of slender *tendrils* instead of blades; in *Cobaea* the tendril ends are recurved somewhat after the fashion of grappling hooks (figs. 266, 267). Tendrils are irritable organs, which react by growth curvatures when they come in contact with a solid object, and thus are enabled to coil about a support. Some petioles (as in *Tropaeolum*) are similarly responsive. Leaf tendrils sometimes have been called modified or metamorphosed leaves or leaflets, a statement that is unwarranted, since there is no evidence that ancestrally they were ever anything else than tendrils.

Petioles. — Attention has been called elsewhere to the chief advantage of leaf-stalks or *petioles*, namely, the facilitation of leaf display to light through elongation and change of orientation. Petioles are poorly developed in most conifers and monocotyls, reaching their culmination in dicotyls, where usually they are slender, elongated organs, contrasting sharply with the blades (fig. 82). Short or broad petioles are of less significance in facilitating leaf display. While many petioles are cylindrical, others are grooved and still



FIGS. 247, 248. — Bud protection in the sycamore (*Platanus occidentalis*); 247, a portion of a twig, showing the swollen base of a petiole; 248, a twig, as in 247, with enough cut away to show the bud for the following year (*d*) covered by the swollen base (*b*) of the petiole (*p*).

others (as in the poplars) are flattened laterally. Some leaves (known as *phyllodes*) consist only of petioles (fig. 159). In some instances petioles are of value in protecting developing buds from transpiration and other detrimental factors, as in *Acer*, *Platanus*, and *Rhus*, where the buds for the next season are hidden more or less completely under the base of the petiole until leaf fall, by which time the bud scales are fully formed (figs. 247, 248). In various developing umbellifer shoots (as in *Angelica*, fig. 249) the petioles have large sheathing bases which en-

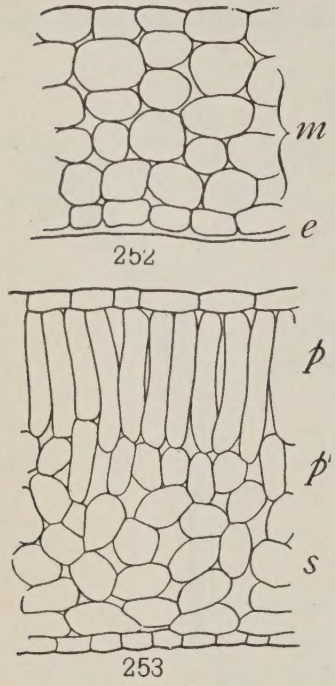


FIGS. 249–251. — 249, a growing shoot of *Angelica atropurpurea*, showing the large inflated petiole (*p*) of a full-grown leaf, from which a young leaf (*l*) is just emerging; the petiole (*p'*) of this young leaf is cut away enough to show within it a still younger leaf (*l'*); the petiole (*p''*) of this younger leaf contains within it a still smaller and younger leaf; 250, a part of a young shoot of a wild pea (*Lathyrus ochroleucus*), showing the prominent stipules (*s*, *s'*), and a young leaf (*l*) terminated by a tendril (*t*); the stipules early develop to their full size, for a time being erect and enclosing an undeveloped shoot, as at *s'*; 251, a growing shoot of a loosestrife (*Lysimachia*), showing a gradual transition from the early scale leaves (*s*) to the foliage leaves (*l*) that appear later; note also the decussate phyllotaxy.

close all the younger parts. In some aquatic plants the petioles are greatly inflated, air-containing organs that help to float the inflorescence (as in *Utricularia inflata*) or the entire plant (as in *Eichhornia*). Variations in the length of petioles, due to external factors, will be considered under stems (p. 243).

Stipules. — Many plants, especially dicotyls, possess leaf appendages known as *stipules*, which usually occur in pairs, one at each side of the petiole near its base. Their presence or absence apparently is unrelated to external factors and often characterizes entire genera or families; the Rosaceae and the Leguminosae, for example, commonly have stipules, while the Cruciferae and the Ranunculaceae commonly have none. Stipules assume different forms, appearing as spines in

Robinia, and as membranous sheaths surrounding the stem in the Polygonaceae (fig. 128), while they are coherent with the petiole in the roses (fig. 401). Stipules may persist through the life of the leaf or they may be *caducous* (*i.e.* falling as the buds open, fig. 255); usually in both cases they are precocious in their development, thus affording some protection to the rest of the developing leaf or shoot from transpiration and other detrimental factors. Probably this is the only rôle of most caducous stipules, and it is well illustrated by the large stipule of *Ficus*, which encloses the developing blade, falling as the latter expands (fig. 15). Many caducous stipules are small and have no apparent rôle. Precocious persistent stipules also may afford protection, as in the peas (figs. 246, 250), where they stand close together vertically, with an undeveloped leaf or shoot enclosed between them; in *Lathyrus ochroleucus*, frosts may kill young parts protruding from the stipules, while not injuring the enclosed parts. The chief rôle of persistent stipules, which, in contrast with caducous stipules, are almost always green, is the manufacture of foods; in plants with large stipules, as in the peas, this rôle assumes quantitative importance, and in *Lathyrus aphaca*, the stipules much surpass the blades in size and in synthetic capacity. If the developing blades of *Prunus serotina* are cut away, the stipules grow to a considerable size and live for a longer time than usual; doubtless they manufacture more food than under ordinary conditions.



FIGS. 252, 253. — Cross sections of leaves of a loosestrife (*Lysimachia*): 252, a section through a scale leaf, showing a relatively undifferentiated mesophyll (*m*), resembling sponge tissue, and the prominently cutinized lower (outer) epidermis (*e*); 253, a section through a foliage leaf, showing a row of conspicuous palisade cells (*p*), a broken row of shorter palisade cells (*p'*), and the sponge tissue (*s*); figs. 252 and 253 highly and equally magnified.

Scale leaves. — *General features.* — *Scale leaves* contain little or no chlorophyll, and hence are not foliage organs; usually they are small yellowish or brownish structures attached to the stem by a broad base, and without prominent veins or leaf teeth; the mesophyll commonly remains undifferentiated through life.

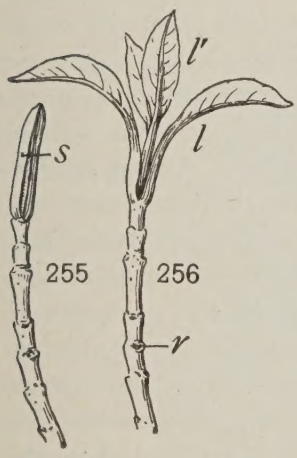
Subterranean scale leaves. — Underground stems, at least when young, are clothed more or less thickly with scale leaves. In bulbs the closely imbricated scale leaves are much thickened, making up the main body of the organ; obviously the rôle of such scale leaves is the accumulation of surplus food and water, which commonly are utilized during subsequent development (fig. 299). The scale leaves of rhizomes are much smaller and thinner than bulb scales, and often are more ephemeral, appearing to have no rôle of importance, except where they protect the growing stem apex as it pushes through the soil (as in *Spartina*, figs. 287, 288).

In many plants with both aerial and subterranean stems (as *Lysimachia*, fig. 251) there are all gradations between scale leaves and foliage leaves, the former having undifferentiated colorless mesophyll, and a strongly cutinized lower epidermis, and

the latter having green palisade and sponge cells (figs. 252, 253). Both kinds of leaves have similar positions and arise from similar primordia. Furthermore, in many cases, foliage leaves develop from scale primordia when exposed from the outset to light and air, and scale leaves may develop in the soil from the primordia of foliage leaves. Thus the distinction between such leaves is not inherent, but a matter of relation to external conditions, though the precise factors involved are imperfectly known.

Bud scales. — In most trees and shrubs of cold and arid climates, buds are formed in the growing season previous to their full development; after reaching a certain size, they remain for some months in comparative quiescence. In most cases the outermost leaf primordia attain their full development the first season, becoming hard and thick scales (figs. 260, 261, 364–366); on the other hand, the innermost primordia beneath the closely imbricated outer scales are incompletely or not at all developed until the following season, when they grow into foliage leaves. *Bud scales* protect the embryonic shoot by reducing transpiration and by minimizing the effect of sudden temperature changes,[1] their thick cutin or cork layer often being supplemented by an external resin coat (as in the cottonwood) or by internal hairs or by both combined (as in the horse chestnut); the scales also are beneficial in protecting the delicate inner portion of the bud from mechanical injuries. The protective efficiency of bud scales is shown by the injury done to germinating buds by a spring frost that would have been harmless if occurring before the shoot had emerged from the scales, though part of the harm is due to the fact that germinating buds contain much more water than do the resting buds, and hence are more subject than the latter to injury through frost. The winter buds of *Viburnum lantanoides* and *Cornus sanguinea* are without scales, the buds of the latter being protected by a dense growth of hairs.

FIG. 254. — A developing shoot of the choke cherry (*Prunus virginiana*), showing a gradual transition from the outer scale leaves (*s*) of the winter buds which are shed early, through the inner scale leaves (*s'*) which elongate as the bud opens, to the ordinary foliage leaves (*l*); note also the slender stipules (*st*).



FIGS. 255, 256. — Shoots of the sweet viburnum (*Viburnum lentago*): 255, a shoot as seen in late winter, showing the two prominent scale leaves (*s*), which enclose the bud; 256, the same shoot in early spring, showing the leaf blades (*l*) which have developed through the renewal of growth in the bud scales (*s* of fig. 255) and also the leaves (*l'*) which have developed from the bud within the scale leaves; note the leaf scars of the previous season (*r*).

[1] The importance of bud scales in protecting from low temperatures often is overestimated; in the winter, ice forms abundantly in the bud tissues.

Bud scales, like subterranean scales, grade into foliage leaves (fig. 254). In the horse chestnut and in various maples the scales represent the basal portion of the leaf, as is shown by the fact that some of the inner scales are tipped by a minute leaf blade (fig. 466). When such a bud germinates, the outer scales drop off, while the inner scales progressively assume more and more the character of foliage leaves, in color and persistence, as well as in shape and size. In *Viburnum lentago* the bud is protected by two large scales with long attenuated tips, which in spring enlarge at the end into small green blades (figs. 255, 256). Not only do such facts show clearly the essential morphological equivalence of foliage leaves and scale leaves, but the identical possibilities of their primordia are capable of experimental demonstration. The removal of the leaves from a pine or lilac shoot while the buds are forming is followed by the development into foliage leaves of primordia that otherwise would become scale leaves, and in most plants the removal of the terminal bud during development is followed by the development into shoots of lateral buds which otherwise would have remained as primordia. Probably, therefore, the stimuli which determine whether primordia develop into bud scales or into foliage leaves are external, but the precise factors involved are unknown. Among the features of buds most in need of explanation are these: the arrest of the shoot primordia at a certain definite stage in development, apparently without external inhibitory influence; the failure of the external leaf primordia to develop into foliage leaves; and the development in unusual thickness of cutin or cork layers on the exposed under surfaces of the scale leaves. Experiment has thrown some light on the cause of arrested shoot development, as will appear elsewhere (p. 250), but why leaf primordia that apparently are exposed to favorable conditions fail to reach their developmental possibilities remains to be explained. Nor is it understood why scales develop cutin in such great amount, when foliage leaves growing under apparently similar conditions exhibit relatively slight cutinization; sometimes (as in *Tilia*) the bud scales have cork as well as cutin, while the foliage leaves have cutin only. It is possible that the relatively high transpiration of late summer is here a factor of importance. Aerial scale leaves, other than those of winter buds, occur in many inflorescences (fig. 257), in various plants without chlorophyll (as *Monotropa*, fig. 411), and even in some green plants (as *Asparagus* and *Equisetum*, figs. 361, 362) in which the stems are the chief synthetic organs.

FIG. 257. — An inflorescence bud of the artichoke (*Cynara scolymus*), showing the overlapping scale leaves (forming an involucre), which protect the delicate flower buds within; the leaves are arranged in many orthostichies, illustrating a phyllotactic system of high rank.

CHAPTER III — STEMS

1. STEMS AS ORGANS OF DISPLAY

General remarks on stems. — Stems are concerned chiefly with reproduction and with the display of other organs, horizontal stems taking the chief part in the former and erect stems in the latter.

FIG. 258. — Palmetto trees (*Sabal palmetto*), illustrating the tree rosette habit and the absence of branching; note the persistent leaf bases which form a protective stem covering; Ocala, Fla. — Photograph by E. W. COWLES.

Though making up the greater part of the stem, the conductive and mechanical tissues may be regarded as structures incident to the display of leaves and reproductive organs, since they give these organs water and mechanical support. Usually the character of the stem determines the form of the plant body, as is indicated by the old and obvious classification of plants into trees, shrubs, and herbs. A *tree*

possesses a tall, woody, perennial stem, usually with a single primary trunk; a *shrub* possesses a similar but smaller stem, usually with a number of approximately equal shoots arising at or near the base; an *herb* is not conspicuously woody and usually has an annual aerial stem and often also a perennial underground stem. These distinctions, however, are arbitrary, gradations between trees and shrubs being common; herbs and shrubs also intergrade, especially in the tropics, where all degrees of woodiness exist and where herbaceous stems often endure for two or more years. Herbs may be subdivided further into forms whose stems are wholly subterranean (as in many ferns), forms whose stems are wholly aerial (as in annuals), forms which have both aerial and subterranean stems (as in most perennials), and forms which apparently are stemless (as in some rosette plants).

The life forms of stems. — The *life form* of a species is the general contour and size of the plant. When woody plants are separated into trees and shrubs the division is based on the life form of the individuals. This character is of importance because the physiognomy or " look " of a plant community is determined by the life forms of the dominant species. Then the life forms of an association are an index of the character of the habitat and more particularly of the nature of the climate. Several systems of life forms have been proposed, all more or less useful, but perhaps the most significant is that devised by Raunkiaer, which is based on stem characters that determine the position in regard to the soil surface of the perennating buds which continue the growth of the plant from season to season. According to this system *stem succulents*, like the cacti, and *true epiphytes*, like the Spanish moss, stand by themselves in two isolated classes, differing markedly from other plants. The other perennial plants, however, form a series of classes whose buds are progressively better protected by their position in regard to the soil surface (fig. 259).

The buds that are least protected are those that occur on stems thrust high into the air. Plants with such buds are termed *phanerophytes* and include *megaphanerophytes*, or tall trees over 30 meters high, *mesophanerophytes*, 8 to 30 meters high, *microphanerophytes*, 2 to 8 meters high, and *nanophanerophytes*, having buds only 0.25 to 2 meters above the ground. The next class is of lower stature than the nanophanerophytes, but has all its buds above the surface of the soil, and such plants are designated *chamaephytes*. Then come *hemicryptophytes* with their buds in the surface layer of the soil and *geophytes*

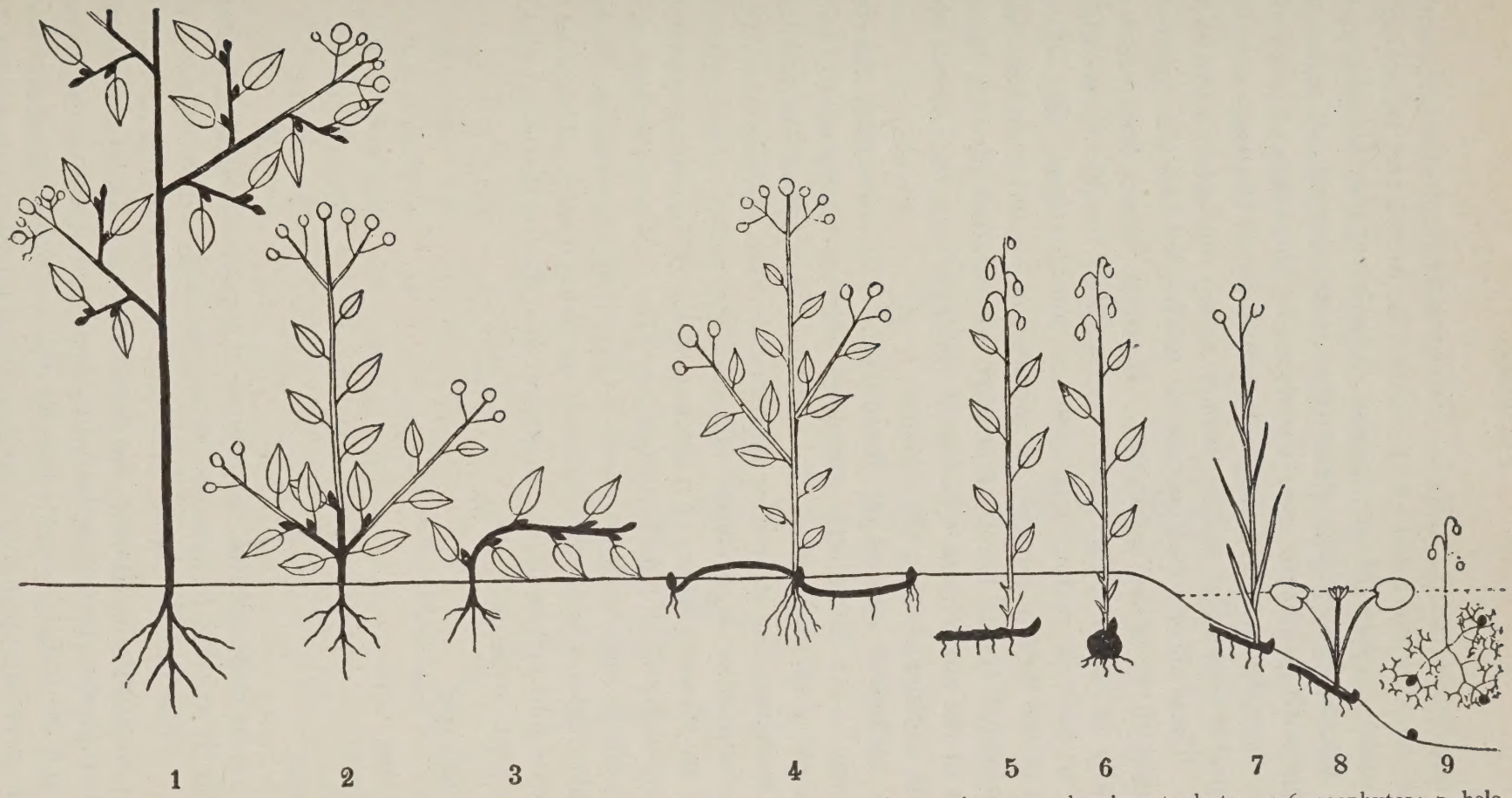


FIG. 259. — Diagrammatic representation of the life forms: 1. phanerophyte; 2–3, chamaephytes; 4, hemicryptophyte; 5–6, geophytes; 7, helophyte; 8–9, hydrophytes. From Ennis after RAUNKIAER.

with buds more deeply buried. The hemicryptophytes include most rosette plants while plants with rootstocks, bulbs, and tubers constitute various types of geophytes. Marsh plants, *helophytes*, and water plants, *hydrophytes*, have their buds covered by water and, together with geophytes, may be termed *cryptophytes*. Finally there are the *therophytes*, or annual plants, which die at the approach of the unfavorable vegetative season through which they pass in the form of seeds. These classes may in turn be subdivided and the system will be found to be quite significant. In every plant association and especially in all the larger plant communities the life forms will be found to exist in various mixtures and combinations. By taking a census of the flora of a region on the basis of life forms and arranging the principal forms on a percentage distribution of the different classes in the entire flora a *biological spectrum* may be formed which gives an excellent key to the climate.

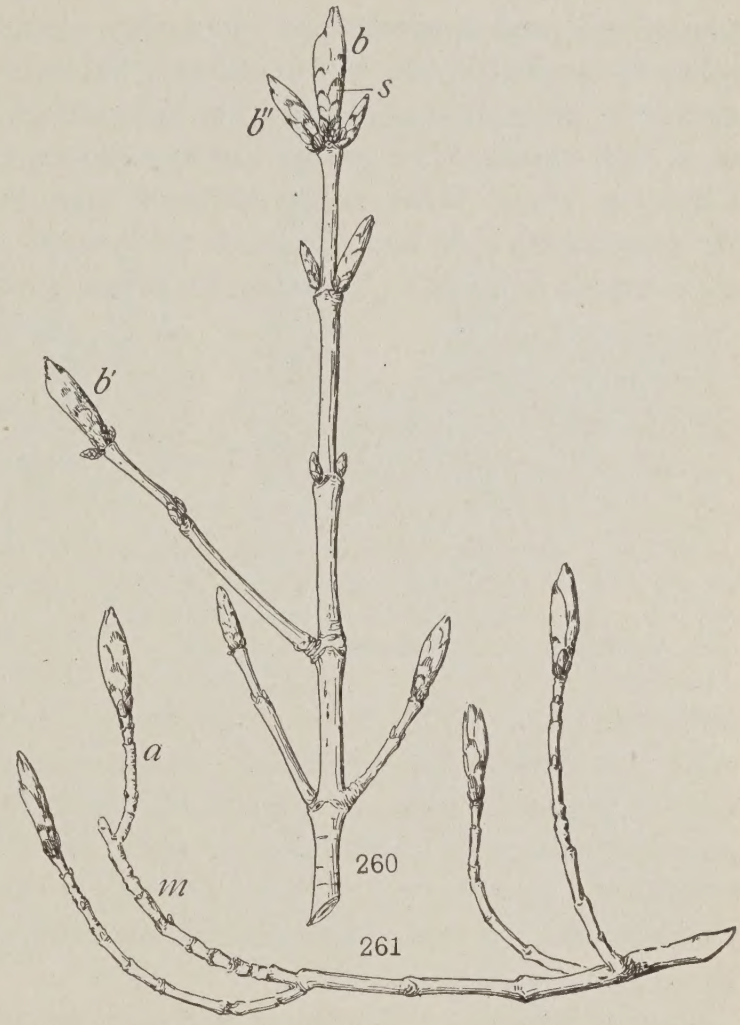
The biological spectra of Raunkiaer. — In arranging the flora according to life forms, in a manner somewhat analogous to the arrangement of the rays of light by a prism, five of the classes are found to be most significant and for convenience each is designated by an appropriate letter here shown following the name. The important classes are phanerophytes (F), chamaephytes (Ch), hemicryptophytes (H), cryptophytes (K), and therophytes (Th). When the flora of the whole world is considered the result is the *normal spectrum*, but for each particular region a somewhat different spectrum results. Omitting the succulents and epiphytes the biological spectra for the world and for some typical areas are:

	F	Ch	H	K	Th
Normal spectrum	46	9	26	6	13
Seychelles	**61**	6	12	5	16
Death Valley, Calif.	26	7	18	7	**42**
Spitzbergen	1	**22**	**60**	15	2
Denmark	7	3	**50**	22	18
Connecticut	15	2	**49**	22	12

According to these spectra the climate of a particular region is characterized by the life form which shows the largest increase over the normal. Thus the Seychelles with their rain forest may be said to have a phanerophytic climate, the desert of Death Valley, California, has a therophytic climate indicated by the large proportion of annual plants, and arctic Spitzbergen, with its cold soil and its great exposure, possesses a hemicryptophytic climate, for the buds of its plants can

neither penetrate the frozen soil nor withstand the cold winds that sweep over its surface.

The display of foliage leaves by stems. — *Elongation and branching.* — From the standpoint of the maximum display of foliage to light and air, the most significant stem features are elongation, branching, and erectness. Elongation is a characteristic feature of most aerial stems, though it is lacking in various rosette plants; growth in height proceeds with extreme slowness in certain other cases, particularly in the cycads, some of which are said to require centuries to reach a height of two or three meters. Branching is relatively slight in the pteridophytes, cycads, and monocotyls (fig. 258), reaching its culmination in the conifers and dicotyls. Thus it appears to be associated with those groups that exhibit considerable growth in diameter from year to year, and it can be recognized readily that the enormous spread of a dicotyl tree would be quite impossible but for such diametral enlargement of the trunk. However, the connection between diametral enlargement and branch-



FIGS. 260, 261. — Twigs of maple (*Acer*): — 260, a terminal twig in its natural position; note the erect terminal bud (*b*) of the main shoot, all other buds being ascending rather than erect, whether they are the terminal buds (*b'*) of lateral shoots or the lateral buds (*b''*) of the main shoot; *s*, bud scales; note that the terminal buds are larger than the lateral buds; 261, a horizontal twig in its natural position; note the ascending curvatures of the main (*m*) and lateral (*a*) shoots.

ing is not absolute, as is indicated by the cycads, which rarely branch, though increasing in stem diameter. Some monocotyls and some extinct pteridophytes exhibit branching or increase in stem diameter or sometimes both combined.

Stem erectness. — Most aerial stems tend to grow erect, being prophototropic and apogeotropic. In a dark chamber, erectness is due solely to apogeotropism, but in ordinary habitats light and gravity cooperate in determining erectness, the light influence being the stronger, as is well shown when plants are exposed to one-sided illumination (figs. 260, 261). When an apogeotropic stem is placed horizontally, the growing tip soon becomes erect, but usually the older parts of the stem remain horizontal; however, in certain grasses (as in the cereals) the whole stem once more becomes erect through differential growth in the lower nodes. Most subterranean stems and some aerial stems, particularly those that are prostrate or running, show little tendency toward erectness (fig. 262). Many of the latter are erect when young and have erect tips through life, suggesting that horizontality in such cases may be due, in part at least, to the lack of sufficient mechanical tissue to permit of erectness. Some fruiting stems grow downward (as in the peanut and in many water plants), while in other water plants (as in *Potamogeton*) the reproductive stems are more rigidly erect than are the vegetative stems.

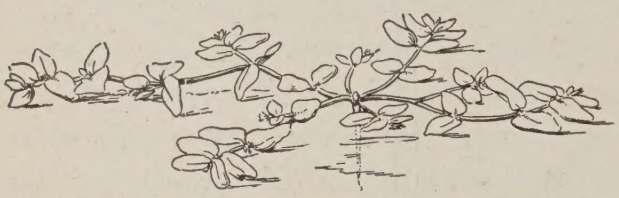


FIG. 262. — A plant of *Euphorbia maculata*, illustrating the prostrate habit; note also that, although the phyllotaxy is decussate, the leaves are in one plane owing to the twisting of the horizontal stems.

Lateral branches. — The most important exception to erectness in aerial stems is in the lateral branches, which grow in various directions, thus resembling the diverse directions of lateral roots. The resulting plant contour usually is symmetrical, especially in those conifers whose trunks are *excurrent* (*i.e.* extending to the summit), and whose outline is approximately an elongated cone (fig. 263). The cause of directional diversity in branching is complicated and but vaguely understood. If the terminal bud of the erect main shoot is removed, certain strong lateral branches hitherto ascending obliquely soon begin to grow erect (as in *Picea*), or buds hitherto inactive develop into erect shoots (as in *Araucaria*). As in roots, the main axis seems to inhibit verti-

cality in the lateral branches. However, aerial stems differ strikingly from roots in that light is an important factor in determining the orientation of lateral branches; lateral stems, even those that descend, usually grow in the direction of maximum incident light.

FIG. 263. — Alpine spruces (*Picea*) and firs (*Abies*), illustrating the spirelike contour and excurrent habit that is characteristic of various conifers of high altitudes; Rocky Mountains, Mont. — Photograph by ELROD.

The advantages of conical shape, elongation, and stem twisting. — Other things being equal, the greater the power of stems to elongate and to branch in diverse directions, the greater is the possibility of maximum foliage display. A broad-based cone, consisting of an excurrent trunk with branches diverging therefrom from base to apex at a constantly decreasing angle, would seem to be the best of all contours for lighting, in proportion to the amount of structural material

involved. Habits of this sort reach their culmination in various arboreal conifers, but are found in scarcely less perfection in some dicotyledonous trees, as the oaks and maples, though in the latter the cones commonly are shorter and broader and often truncated (figs. 150, 151). In many alpine conifers (fig. 263) and in various trees of warm

FIG. 264. — A bur oak tree (*Quercus macrocarpa*) in winter, showing representative deliquescence; note the tortuous branching characteristic of this species of oak; Chicago, Ill. — Photograph by LAND.

climates (as the cypress and Lombardy poplar), the stem contour is a narrow, elongated cone; it has been suggested that such shapes are well-fitted for protection from intense light. The display of foliage also is facilitated in high degree by the variability of the internodes in respect to length, a variability comparable to that of petioles and attended with similar advantages (see p. 240 for discussion of causes).

Internodal elongation makes possible not only the prevention of shading in large-leaved plants, but also, in many cases, the elevation of plants above their surroundings. In horizontal stems, leaf display often is facilitated by stem twisting, through which the leaves are brought into a common plane transverse to incident light (fig. 84).

Stem contours other than conical. — Though the prevailing tree contour is conical, there are many exceptions, particularly among *deliquescent* trees (*i.e.* trees whose main stem is replaced by the diverging upper lateral branches), such as the bur oak (fig. 264), the silver maple, and especially the American elm, whose shape is that of a flaring vase. A prevalence of horizontal branching characterizes the cedar of Lebanon, while some hawthorns and acacias have an almost umbrella-like contour, owing to the numerous descending branches. The extreme drooping of the branches in the weeping willow (due, perhaps, to a slight development of mechanical tissue) gives a characteristic rounded contour to the crown. Many trees, especially willows, are asymmetric, the main trunks curving to one side as they develop. So far as known, these diverse tree shapes are not inherently advantageous. The causes are quite as little known, though much more likely to repay investigation. In some cases, as in *Araucaria* and *Pinus strobus*, the branches appear to be in whorls, the tree thus being divided into stories; this habit results from the development at intervals of numbers of lateral buds. An interesting habit is that of the rosette-bearing trees (as in the ferns, cycads, and palms, fig. 258), characteristic of tropical forests. While the lack of branches in such plants appears disadvantageous, the elevation of the crown of leaves makes possible a relatively favorable display of foliage. The palmetto often has a short trunk or none at all in dry open habitats, while it has a tall slender trunk in deep woods.

Foliage display in shrubs and herbs. — Most shrubs and herbs that have aerial stems exhibit essentially the same methods of display as do trees, their branches ascending or diverging variously and exhibiting conical and other contours. Herbs with stems wholly underground are poorly situated for leaf display, though some forms (as *Pteris*) have greatly elongated petioles, which raise the leaf blades well into the light. Rosette plants also are situated somewhat poorly for light reception, though the leaves originate above the soil level instead of below it.

The significance of trees and grasses in foliage display. — Trees are the culminating forms of the plant world from the standpoint of stem development and the display of foliage to light, their great height and size making possible the development and adequate display of an enormous number of leaves. Their height and size in turn are made possible by the perennial nature of their aerial stems, which permits each season the resumption of growth where it ceased the year before, and also by their diametral increase, which permits the development of a supporting trunk sufficient to bear the weight of the constantly

increasing branches. Trees dominate the vegetation in most regions where they grow, other plants being eliminated except such as can endure the shade; among trees those dominate ultimately whose seedlings can germinate in the shade. In prairies and in treeless swamps, however, there is a predominance of sun-requiring herbs, among which rhizomatous monocotyls, such as many grasses, sedges, and rushes, take a prominent place. Perhaps from the standpoint of world dominance plants with grasslike foliage may be placed second only to the trees. From the foregoing the conclusion must not be drawn that plants other than trees and grasses are without comparative advantage. Of all vegetative organs the leaves of trees are the farthest removed from the water supply and the most exposed to the dangers of transpiration. Thus the tree habit is possible only through the development of extensive conductive, mechanical, and protective tissues.

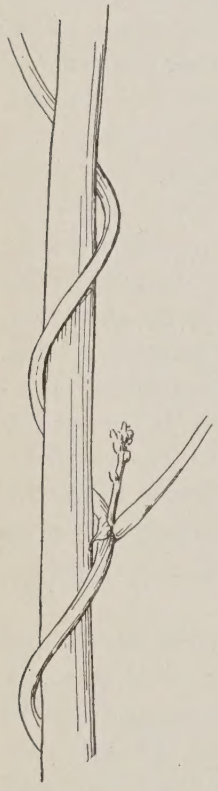
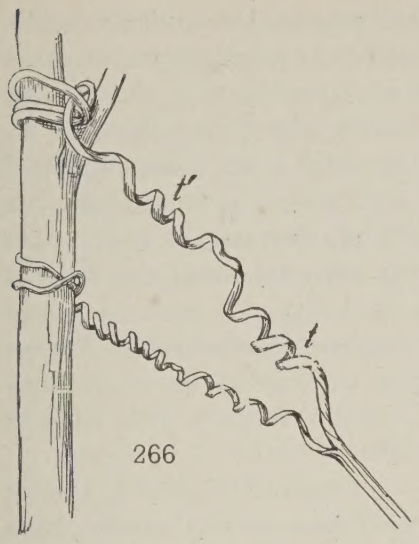


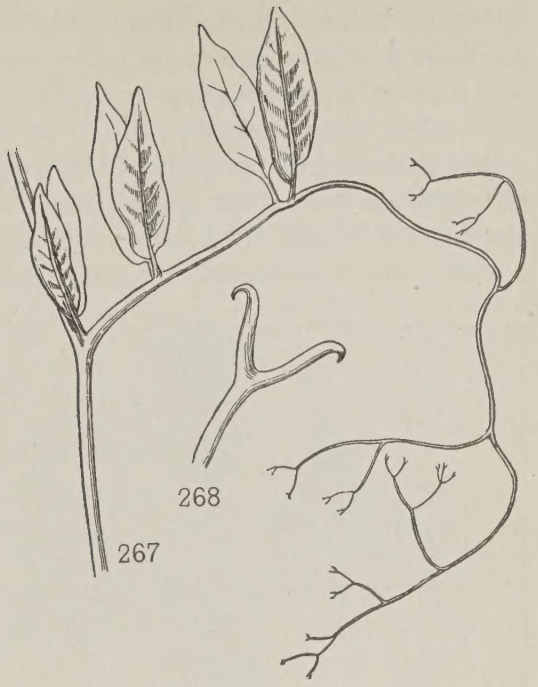
FIG. 265. — A part of the climbing stem of a scarlet runner bean (*Phaseolus multiflorus*), a representative sinistrorse twiner.

Lianas in relation to leaf display. — *Definition of lianas.* — *Lianas* are plants that ascend by climbing or by leaning upon other plants or upon any adequate support, their mechanical tissue being insufficient to permit them to stand erect, though they are prophototropic and apogeotropic.

Twiners. — Possibly the most specialized climbers are those that *twine*, for in them the growing tip of the main stem executes movements, known as revolving nutations, whereby a widening circumference comes within the sweep of the elongating stem. After coming into contact with an erect stem, the continuation of the nutatory movements results in twining.

If the lower part of a coil appears from behind the support at the observer's left and the upper part disappears at his right, the twiner is called *sinistrorse* (as in the bean, fig. 265, and in the dodder, fig. 388). If, as is more rarely the case, the lower part of a coil appears at the right and the upper part disappears at the left, the twiner is called *dextrorse* (as in the hop). Common native twiners are the bittersweet (*Celastrus*) and the dodder (*Cuscuta*), the latter being a parasite in which contact stimulation incites the development of sucking organs (haustoria) that serve also to hold the climber firmly to the supporting plant. In twiners and in other lianas there is a striking development of conductive tissues (p. 204).

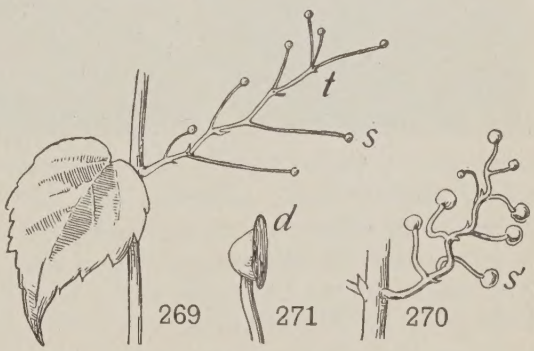




FIGS. 266–268. — 266, tendrils of a wild cucumber (*Echinocystis lobata*); note the reverse directions of the spirals, those at *t* being dextrorse and those at *t'* sinistrorse; note also the coiling of the tendril ends about the support; 267, 268, tendrils of *Cobaea scandens;* 267, a compound leaf with three pairs of leaflets and a terminal dichotomously branched tendril; 268, the tip of one of the tendril branches considerably magnified, showing the recurved hooks which hold the plant to a support.

Tendril climbers. — Scarcely second to twiners in specialization are the *tendril climbers*, the tendril commonly being an organ homologous with leaves or leaflets (figs. 267, 268, 246, 250), or with branches (as in the passion flowers and grapes, figs. 269, 270); or tendrils may be organs of doubtful homology (as in the pumpkin family, fig. 266). Tendrils may be simple or forked and commonly are sensitive to contact, coiling about their support; in *Sicyos* the sensitiveness is so great that the slightest friction incites differential growth, resulting after a few moments in conspicuous curvature.

The region of sensitiveness may be somewhat extensive, or (as in the pumpkin family) confined to certain areas, known as *tactile spots*, where there may be thin places or slight



FIGS. 269–271. — Tendrils of the Japan ivy (*Psedera tricuspidata*): 269, a portion of a stem, showing a young tendril (*t*), the branches having small globular swellings (*s*) at the tip; 270, a similar tendril at maturity, the swollen tips (*s'*) being much larger, and also flattened on one side in contact with the support; 271, a mature tendril tip, somewhat magnified, showing the adhesive disk (*d*), which may fasten even to a smooth surface.

elevations in the outer epidermal wall; the tendrils that react most quickly usually are those that have localized sensitive regions. Soon after tendrils become attached to a support, spiral coils appear in the unattached portions (fig. 266), and the tendril-bearing plant is drawn close to its support; mechanical tissues also may develop, increasing the strength of the tendril (p. 214). One of the most specialized of tendrils is that of the Japan ivy (*Psedera tricuspidata*); the tendril branches terminate in knobs, which upon contact broaden out into disk-shaped suckers that secrete a mucilaginous substance and thereby adhere most tenaciously to walls or bark (figs. 269–271). A variety of the Virginia creeper (*Psedera quinquefolia*) has somewhat similar tendrils with *adhesive disks*.

FIG. 272. — A fern (*Nephrolepis*) as a rhizome climber on the palmetto (*Sabal palmetto*); note that the fern occurs at the upper part of the trunk where the leaf bases persist; the rhizome dies below and ascends *pari passu* with the developing palm; Miami, Fla. — Photograph by E. W. COWLES.

Plants which climb by roots or rhizomes. — *Root climbers* have been considered elsewhere, and it has been noted that anchoring roots, like tendrils, often are sensitive to mechanical stimulation, and that such roots frequently grow horizontally about their support instead of growing downward as do most roots. Root climbers (as the English ivy) are quite as able to adhere to vertical walls as are those plants whose tendrils have adhesive disks. The Virginia creeper sometimes climbs by roots as well as by tendrils with adhesive disks. The elongating rhizomes of various tropical ferns (as *Nephrolepis*) often come in contact with tree trunks, which they may ascend, especially if the bark is spongy and easily penetrated (as in the palmetto). If the rhizome continues to ascend, its ground connections may be severed through the decay of the posterior portions, thus resulting in the transformation of a soil plant into an epiphyte or an epiphytic liana, though the roots, whether in the soil or in the bark, are true soil roots, which absorb water and salts from the substratum (fig. 272). Such climbing rhizomes often keep pace with the ascent of the supporting tree, and in the palmetto they are found most commonly in the enlarged spongy region just below the leaf crown. The rhizome of *Polypodium aureum* often creeps around palmetto trunks in a slowly ascending spiral. *Rhizome climbers* do not always start from the ground, since spores may germinate at any level on the trunk. Outside

of the tropics climbing by rhizomes is illustrated by several species of *Polypodium;* various creeping mosses and liverworts ascend tree trunks in similar fashion, especially in swamps, and embedded in the mosses there occasionally may be seen such rhizomes as those of *Maianthemum.*

Plants which climb by hooks or thorns. — In *hook climbers* and *thorn climbers* attachment or connection with a support is in a sense accidental, involving no special growth features as in the previous groups of lianas. Climbing by thorns is seen in roses, in blackberries, and in the greenbrier; the last, however, is supported much more effectively by tendrils. Hooks that point downward characterize various bedstraws (*Galium*) and the hop (fig. 273), and are superior to thorns in that they prevent slipping backward.

Leaners. — A transition between lianas and ordinary erect plants is afforded by one of the night-shades, *Solanum dulcamara,* which leans on neighboring plants, having no means for climbing, except that it sometimes twines to a slight extent. Such a plant may be called a *leaner.* The tall nasturtium (*Tropaeolum*) is another such leaner, which also may climb to some extent by petiole twisting. Many plants that are prostrate in the open may be leaners where the vegetation is dense. Closely related to leaners are those submersed aquatics whose stems are supported by the water, their mechanical tissue being insufficient to keep the plants erect.

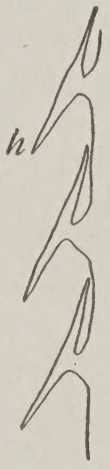


FIG. 273. — A diagrammatic longitudinal section through the outer portion of a hop stem (*Humulus lupulus*), showing emergences with obliquely oriented barbs, the lower ones (*h*) pointing downward and outward in such a way as to hold the stem to a support; somewhat magnified.

The advantages and disadvantages of the liana habit. — The great advantage possessed by lianas is their favorable position for foliage display without the construction of a large amount of supporting tissue. When a vine sprawls over a hawthorn, the liana may have a foliage display equal to that of the tree. However, this habit may be accompanied by ultimate disadvantage, because the leaves of the liana cut off the light from the leaves of the supporting tree; also the weight of the vine may become too great for the tree, resulting in the downfall of both (fig. 274). The collapse of a branch may suffice for the downfall of a tendril climber; the stems of woody twiners sometimes are ruptured by the increasing pressure to which they are subjected by the diametral enlargement of the tree, though more commonly the twining stem becomes embedded in the growing trunk.

The origin and distribution of lianas. — While herbaceous lianas may occur almost anywhere, woody lianas are associated peculiarly

with forests, reaching their culmination in the tropics, where there exist all but impenetrable tangles of intertwining vines, some of which (as the rattan palm) may reach the great length of 250 meters, that is, equal to twice the height of the tallest trees (fig. 275). In temperate regions lianas culminate in the rich soil along rivers, the greenbrier

FIG. 274. — A grape-vine (*Vitis*) that has clambered over a hawthorn (*Crataegus*) and occasioned its destruction; in the left foreground is a cottonwood (*Populus deltoides*) and in the left background is an elm (*Ulmus americana*); River Forest, Ill. — Photograph by LAND.

thickets with their thorns approaching the impenetrability of tropical tangles. It is assumed, and probably correctly, that lianas have come from erect ancestors, and that their evolution was subsequent to that of trees, although potential lianas well may have existed before trees and even may have climbed over rock cliffs. Probably the first lianas were leaners, the twiners and tendril climbers developing later. It is the prevalent view that lianas have resulted from the " struggle

for light " in the forest. Of this there is no evidence whatever, except in so far as stems in general tend to elongate where there is decreased light (p. 240).

Pendulous plants. — Various vines, as the Virginia creeper, if rooted at the top of a narrow cañon, may hang down over the wall; however, such vines are prophototropic and apogeotropic, as may be seen by the recurved tips, and by the petioles

FIG. 275. — A tropical mesophytic forest, rich in lianas; at the left is a sinistrorse twiner; note the twisting of the liana stems at the center; the dominating liana is *Agelaea wallichii*, but in the undergrowth are many rattan palms (*Calamus*), which at first are ordinary palm rosettes, but later develop into lianas of extraordinary length; Lamao Forest Reserve, Philippine Islands. — From WHITFORD (Courtesy of the Philippine Bureau of Forestry).

which point upward toward the light (fig. 276). Leaners sometimes behave similarly, the most remarkable feature being that the pendulous stems are several times as long as are erect stems in the same species (as in *Rubus occidentalis* and *Ribes cynosbati*). The cause of this elongation is unknown, though it seems possible that it is in some way associated with the fact that growth is in the direction of the gravity pull, instead of against it, as in erect stems. It has been found that when growing stems are subjected to tension, cell elongation takes place in the direction of the pull.

Epiphytes. — *General remarks.* — *Epiphytes* are nutritively independent plants, which are given complete mechanical support by other plants, differing from parasites in not deriving food or water from the supporting plant, and from lianas in having no soil connections. Although all gradations exist between lianas, epiphytes, and ordinary soil plants (as in *Nephrolepis*, p. 170), the most representative epiphytic forms occur only as epiphytes. In regions with winters or with prolonged dry periods, true epiphytes are limited essentially to algae, lichens, liverworts, and mosses; in the moist tropics, these forms are supplemented by many ferns and seed plants, especially orchids and bromelias (fig. 277). In many tropical forests the epiphytes are arranged in stories or strata; those in the tree tops (such as species of *Tillandsia*) are very xerophytic in structure, while farther down are more mesophytic forms, such as the orchids and ferns. Near the ground, where desiccation rarely takes place, there occur extreme mesophytes, such as the filmy ferns. The xerophytic forms of the tree tops of moist regions penetrate farther into dry regions than do other epiphytes. Even in northern forests a similar stratification exists, xerophytic lichens occurring in the branches, while farther down are mosses and liverworts. Probably the absence of epiphytic seed plants and ferns in most dry and cold climates is due to the long period of excessive transpiration with little or no aerial absorption, characteristic of such climates. The most northern of such epiphytes in the eastern United States, *Tillandsia usneoides* (fig. 209) and *Polypodium polypodioides*, in their structural features and life habits are most pronounced xerophytes. Even mosses and lichens as epiphytes are much more abundant in humid climates than elsewhere.

FIG. 276. — A pendulous stem of the Virginia creeper (*Psedera quinquefolia*), showing the curvature of lateral branches upward toward the light; note the conspicuous leaf scars (*r*) of the previous season.

Structures characterizing epiphytes. — Epiphytes commonly are characterized by highly specialized organs of absorption, or by structures which effectively reduce transpiration or accumulate large quantities of water. The absorptive organs of epiphytes, as seen in the lichen

thallus, in the aerial roots of orchids, and in the leaves of mosses and bromelias, have been treated elsewhere. Most orchids and bromelias have highly cutinized epidermal walls, which, with other protective features, reduce transpiration to such an extent that the plants do not dry out for weeks. In many orchids the leaves or stems or both are

FIG. 277. — Epiphytes on a live oak (*Quercus virginiana*), the dominating form being a species of *Tillandsia;* Miami, Fla. — Photograph by MEYERS.

greatly thickened and contain large quantities of water, the stems frequently showing bulbous enlargement. In most bromelias the leaves form a sort of cistern, which retains water for weeks after a rain; since these *cistern epiphytes* absorb water almost entirely through the leaves, the advantage of the habit is obvious.

Epiphylls; injury due to epiphytes. — Epiphytes occurring on leaves are known as *epiphylls* (fig. 278), and are especially characteristic of the moist tropics; lichens,

mosses, and even vascular plants occur in this strange position. Epiphylls are very injurious to the leaves on which they grow, cutting off light and impeding gas exchange. Epiphyllous lichens show all gradations between epiphytism and parasitism, some forms being strictly external to the leaf, while other forms destroy the cuticle and thus have position directly on the outer wall of the epidermis; in still other cases (as in *Strigula*) the lichen tissues may penetrate the mesophyll. Stem epiphytes also often injure their supporting plants, checking gas exchanges through the bark or breaking the branches by their weight. Even in cold climates the beard lichens (such as *Usnea* and *Alectoria*) may enfold the leafy twigs of conifers to such an extent as to cause their death; in some cases the hyphae of *Usnea* penetrate the living cells of the supporting plant.

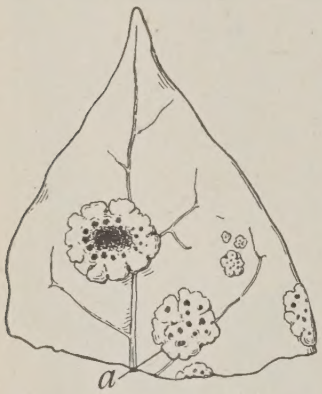


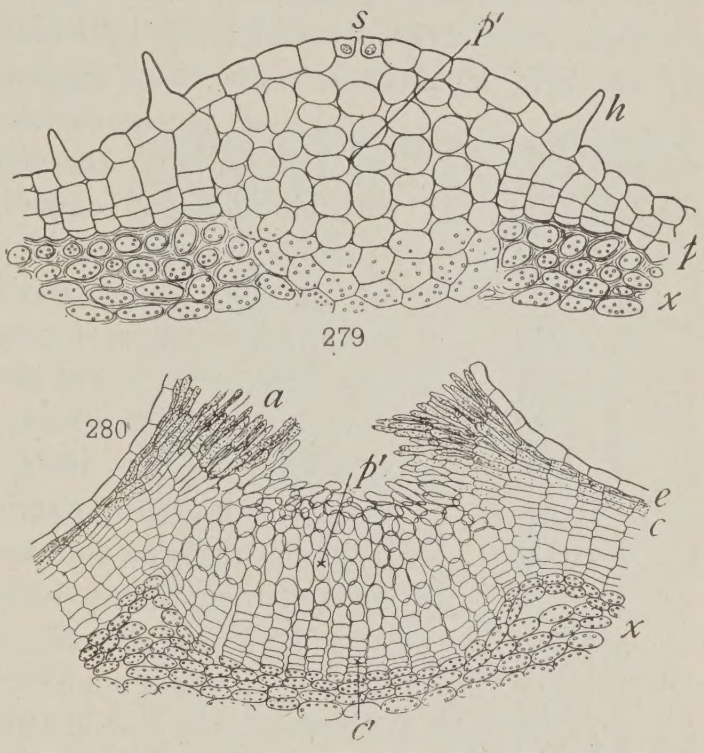
FIG. 278. — Epiphyllous foliose lichens (*Strigula complanata*) on a leaf of *Ocotea*; *a*, fruit dots (apothecia); such lichens propagate radially and the largest one here figured already has disorganized at the older central portion, the thallus becoming ring-shaped instead of solid.

Subordinate categories of epiphytes. — Plants epiphytic for only a part of their existence (as *Ficus*, p. 31) are known as *hemiepiphytes*. In temperate regions many ordinary soil plants are found in the crotches of trees, where a little soil has collected; such plants may be called *pseudoepiphytes*. Various algae occur as epiphytes in the water, but most forms grow equally well when attached to rocks or shells; however, for species requiring considerable light, attachment to plant organs which float near the surface may be advantageous. Various epiphytic lichens and mosses occur also as *lithophytes*, and *Tillandsia* may grow even on telegraph wires.

Restriction of epiphytes to particular supports. — Most true epiphytes are restricted to trees, some being confined to particular species. Among the lichens some crustose species (as *Graphis scripta*) grow chiefly on smooth-barked trees. The palmetto has certain characteristic epiphytes that rarely if ever grow on other trees; probably this is because its soft spongy bark especially facilitates attachment. Possibly some epiphytes have chemical as well as mechanical relations with trees, certain bark substances, perhaps, furnishing a necessary food element or neutralizing root excreta; perhaps the bark of some trees may contain substances injurious to the roots of certain epiphytes.

The advantages and disadvantages of epiphytism. — It is difficult to see any great advantage in the epiphytic habit other than that epiphytes are relatively exempt from the extreme overcrowding which characterizes soil plants. It is usual to class epiphytes with lianas as a group developed in the " struggle for light," but there is no evidence therefor; furthermore, epiphytes occur chiefly on trunks and branches which are lighted scarcely better than the ground. The disadvantages of the epiphytic habit, namely, restricted absorption and exposure to

high transpiration, are very obvious. The underlying causes of epiphytism are unknown, though *facultative epiphytes*, such as *Nephrolepis*, suggest possible beginnings. The bromelia series (p. 130) is continuous from the non-epiphytic pineapple through the leafy species of *Tillandsia* (as *T. utriculata*) to the leafless *T. usneoides* and may represent a line of progress toward *obligate* xerophytic epiphytism.



FIGS. 279, 280. — Lenticels: 279, a young lenticel as seen in a cross section through the outer part of a growing stem of the privet (*Ligustrum vulgare*); *s*, a stoma beneath which a lenticel is developing; *p*, the phellogen layer from which a closing layer of cork later develops; *x*, chlorenchyma, composed of thin-walled cells beneath the lenticel and of thick-walled cells elsewhere; *h*, epidermal hairs; 280, a cross section through the outer part of a stem of an elder (*Sambucus nigra*), showing a lenticel during the summer of its second year; *e*, epidermis; *c*, cork layer of the preceding year, which has been ruptured at *a* by the development of complementary tissue (*p'*); *c'*, developing cork layer of the current season; *x*, chlorenchyma; both figures highly magnified. — Fig. 280 from HABERLANDT.

Carbohydrate synthesis and aeration in stems. — *Stem chlorophyll.* — In addition to being organs of foliage display, stems are important food-making organs. Young woody stems, as well as herbaceous stems, commonly are green, though the total expanse of chlorophyll tissue in stems is much less than in leaves. The chlorophyll occurs in the cortex, gradually decreasing inwards, as in thick leaves; sometimes (as in most leafless stems) the outermost layers are differentiated into palisade cells. As in leaves, there are internal air chambers and stomata, which act as passageways for gases. In many water plants there are capacious air chambers, which are separated from one another by diaphragms (fig. 95) or by solid nodes that strengthen the stem. During the first year a thick bark develops in woody stems, largely

through the formation of new cells and the subsequent modification of their walls. The stems in most instances no longer appear green; nevertheless beneath the outer bark there is green tissue that is of great interest because of the relative darkness in which chlorophyll is developed and food is manufactured (figs. 279, 340). As the bark increases in thickness, the chlorophyll gradually decreases, finally disappearing from old stems. It has been suggested that the food-making activity of deciduous trees may not cease upon leaf fall, but that the stem chlorophyll, like the leaf chlorophyll of conifers, may manufacture food at temperatures favorable for synthesis during the late autumn, winter, and early spring.

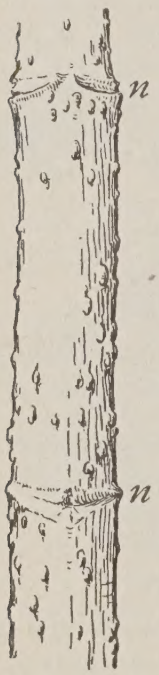


FIG. 281. — A portion of the stem of *Bryophyllum calycinum*, showing an abundant development of warty emergences, the lenticels; note also the leaf scars at the nodes (*n*).

The structural features of lenticels. — During the first vegetative period of a woody stem, a cork cambium or phellogen layer (p. 220) makes its appearance in the cortex, giving rise to a protective cylinder of cork, which cuts off communication between the cortex and the stomata. Underneath some of the stomata, however, cork does not develop for a time, the phellogen giving rise instead to a loose tissue composed of rounded cells, the *complementary cells*, between which are conspicuous air spaces (figs. 279, 280). This tissue, by reason of the cell turgidity and the air spaces, takes up much more space than does the cork, rarely having adequate room for full development beneath the epidermis. Consequently the epidermis is soon ruptured and the complementary tissue protrudes, forming with the upturned ruptured edges a characteristic emergence visible to the unaided eye (figs. 281, 364–366); the entire structure, of which the loose complementary tissue forms the most significant part, is known as a *lenticel*. Though lenticels in some species remain open for many years through the continued formation of complementary cells from phellogen, in most plants the cork cylinder eventually becomes continuous through cork formation underneath the lenticels; often this cork is more permeable than ordinary cork, on account of the presence of intercellular air spaces. In many plants closure occurs in the autumn, the lenticels being essentially

cut off from the cortex before winter. Such lenticels may remain permanently closed, or the following spring the development of complementary cells underneath the cork may cause it to burst, thus reopening the lenticels to gas exchange. In most woody plants the lenticels are roundish or slightly elongated structures which disappear after a few years by reason of bark exfoliation, but in the birches and in some cherries they remain for many years, elongating horizontally as the trunk increases in diameter (fig. 282). In some woody stems, as in the grape, lenticels do not occur.

FIG. 282. — Trunks of the paper birch (*Betula alba papyrifera*), showing numerous transversely elongated permanent lenticels; Salisbury, Conn. — Photograph by E. W. COWLES.

The causes of lenticel development. — The development of cork from phellogen is favored by desiccation (p. 221), while the presence of abundant water causes the development of a loose tissue with prominent air spaces, the aerenchyma (p. 68). The complementary tissue of lenticels, like aerenchyma, is derived from phellogen, and the cause of its development has been discovered to be similar, while subsequent closure through cork development is due to desiccation. In some plants cork and complementary tissue develop alternately, the reason apparently being that lenticel closure checks transpiration and permits water accumulation and the consequent development of complementary tissue, which bursts through the cork and opens the lenticel. Then active transpiration again takes place, desiccation ensues, and a cork layer once more develops.

When a woody stem (as in the willow) is submersed, the tissues usually become surcharged with water, and complementary cells develop from the phellogen to such an extent that they burst through the bark (particularly at the lenticels, because they are the points of least resistance), forming whitish patches, the so-called *water lenticels*, which differ from ordinary lenticels only in that the greater water supply causes larger emergences.

The rôle of lenticels. — Lenticels are regions of gas exchange, taking the place of stomata in stems after the inception of secondary growth, and making possible the continued activity of the chlorophyll after cork formation has begun. Only a somewhat structureless organ such as a lenticel, consisting of an indefinite patch of loose cells, is fitted for gas exchange in bark, where growth and rupture occur continually. Lenticel closure involves a decrease in gas exchange, hence reducing synthesis and perhaps retarding respiration; however, as closure occurs chiefly at the inception of dry or cold weather, it is likely that the gain from the reduction of transpiration is greater than the loss resulting from decreased synthesis. Probably the small amount of oxygen used in respiration is obtained in part through the bark, which is not wholly impermeable; the lenticels, even when closed, are more permeable than other regions of the bark.

After the lenticels disappear, the bark continues to increase in thickness, gas exchange becoming less and less, until it ceases to be appreciable, except, perhaps, beneath furrows, where the protective layers are thin and frequently ruptured by stem enlargement. It has been suggested, however, that the death of trees partly submerged by water or by dune sand is due to the checking of stem respiration, thus assuming that gas exchange through bark may not be inconsequential, though in such cases death may be due to the cutting off of oxygen from the roots; in any event, continued vigor characterizes trees like the willows and poplars, in which submergence by water or sand incites the development of adventitious roots on the buried stems, while oaks and pines, having no capacity to develop such adventitious roots, soon die.

The distribution of lenticels. — No systematic study has been made of lenticel distribution. Usually lenticels are most abundant just beneath the nodes. In some trees, as *Gleditsia*, they are more numerous on the under side of horizontal branches, while occurring equally on all sides of vertical branches.

Carbohydrate synthesis in leafless stems. — From the standpoint of synthesis the most important stems are those on which leaves are insignificant or wholly absent, for here the stem becomes the chief food-making organ. This habit is well illustrated by the cacti, whose stems may be flattened (*Opuntia*, figs. 347–349), cylindrical (*Cereus*, fig. 342), or spherical (*Echinocactus*, fig. 370); the stem of *Echinocactus* with its small surface in proportion to its volume represents the extreme antithesis of the forest mesophyte with its expanded leaves. Such stems contrast with ordinary leaf-bearing green stems in possessing strong palisades in place of weak palisades or sponge tissue. The chlorophyll also extends much deeper than in most stems and leaves,

FIG. 283. — *Ephedra trifurca*, a desert switch plant, with numerous green leafless switchlike branches; the structures on the branches are reproductive organs; Mesilla, New Mexico. — Photograph by LAND.

reaching the great depth of 6.5 mm. in *Cereus giganteus*. Synthetically comparable to cacti are many *switch plants*, with numerous leafless switchlike stems (as in *Ephedra*, fig. 283). Some switch plants, as *Spartium* and *Cytisus*, have small leaves, which have been shown to equal or surpass the stems in synthetic activity.

FIG. 284. — A colony of bulrushes (*Scirpus validus*); though the habit of an individual shoot is that of an extreme xerophyte well fitted for protection from intense light, a crowded colony of such shoots is fitted for optimum lighting; Selkirk, Manitoba. — Photograph by E. W. COWLES.

Asparagus and *Casuarina* have numerous slender branches, which give the aspect of delicate foliage. *Equisetum* (figs. 361, 362) is a characteristic leafless herb. In *Muehlenbeckia* the stems, though vertical, are much flattened, and in *Myrsiphyllum*, *Ruscus*, and *Phyllocladus* they quite resemble leaves and are called *phylloclades*. Many such plants have prominent leaves in the seedling stages, suggesting, according to the recapitulation theory, that various leafless xerophytes may have been derived from a mesophytic leafy ancestry; the phylloclade forms have been thought to represent a subsequent return to more mesophytic structures.

Not all leafless stems are xerophytic. Such representative swamp plants as the rushes (*Juncus*, *Scirpus*, *Eleocharis*) often are essentially

leafless, the synthesis of foods being here a stem function, as in the cacti (fig. 284). In their high cutinization and prominent palisades such plants resemble xerophytes, but they are quite unlike them in their abundance of air spaces and in their high transpiration. It has been suggested that their exposure to intense light, reflected as well as direct, makes verticality almost as advantageous as in xerophytic habitats. It is much more likely that in rushes, as in swamp grasses and in flags, verticality is advantageous, because it permits a maximum display to light where growth is dense. Whatever may be the causes or advantages, it certainly is striking that leafless stems with a relative maximum of stem synthesis occur in such opposite habitats as deserts and swamps, and that the vertical habit which means minimum light exposure and maximum protection for the desert individual means maximum light exposure for the mass of vegetation in the swamp.

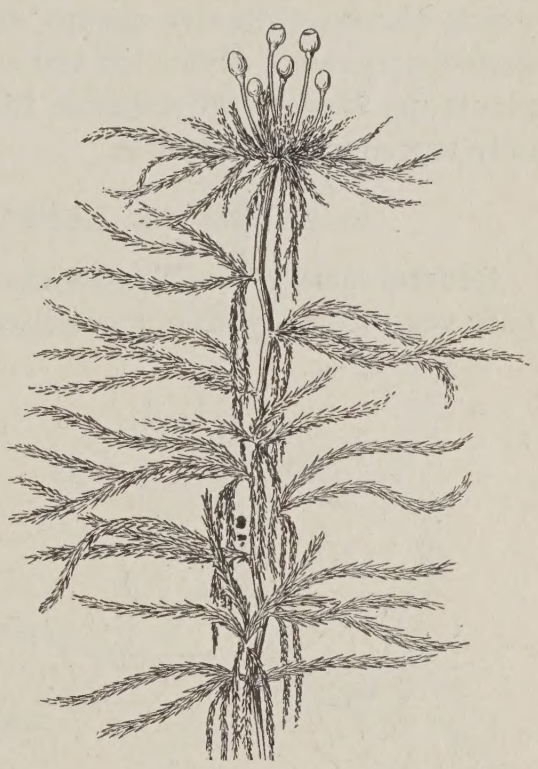


FIG. 285. — The upper part of a gametophytic stem of *Sphagnum*, above which is displayed a terminal cluster of sporophytes with their spore-bearing organs; note the descending gametophytic branches, which facilitate the ascent of water by capillarity. — From COULTER (Vol. One).

The display of reproductive organs by stems. — In the lower groups, stems seem to be associated with the display of reproductive rather than synthetic organs, the obvious advantage being the facilitation of spore dispersal by wind and by other agents. In the fungi, where carbohydrate synthesis does not take place, there are prominent stalks or *stipes* tipped by the spore-bearing organs (as in various molds and toadstools, figs. 385, 428). While the leafy shoots and thalli of liverworts generally are closely appressed to the substratum, most species have stalked spore-bearing organs that facilitate dispersal. In the mosses the organ (*seta*) that bears the capsule with its asexual spores is elevated above the rest of the plant (fig. 285). In the pteridophytes the sporangia

may be borne on ordinary leaves or on special leaves or stems (as in *Osmunda*, *Equisetum*, *Lycopodium*). In the seed plants the display of reproductive organs may be still more advantageous than in the lower groups, by reason of the important part played by insects in pollination and by birds in seed dispersal. Even rosette plants (as *Taraxacum* and *Agave*, figs. 175, 228) usually have tall stalks on which the reproductive organs are borne. In some aquatics the flowers are erected above the water on special stems. Colorless seed plants (as *Monotropa*) resemble fungi in having stems that display only reproductive organs.

2. STEMS AS REPRODUCTIVE ORGANS

General remarks. — Plants spread in various ways, involving ordinary vegetative organs or specialized organs, such as seeds and spores. While the latter are the more effective dispersing agents over great distances, vegetative reproduction is much more effective as a means of occupying the ground in the immediate vicinity of the parent plant. Among such organs of vegetative reproduction stems take the foremost place.

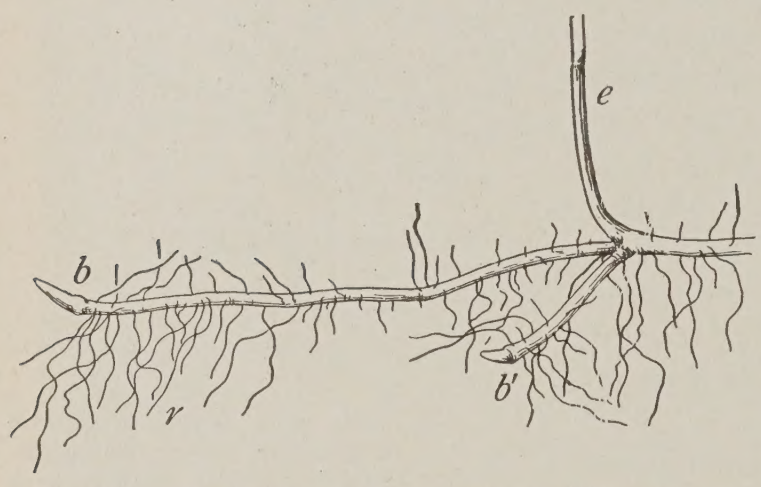
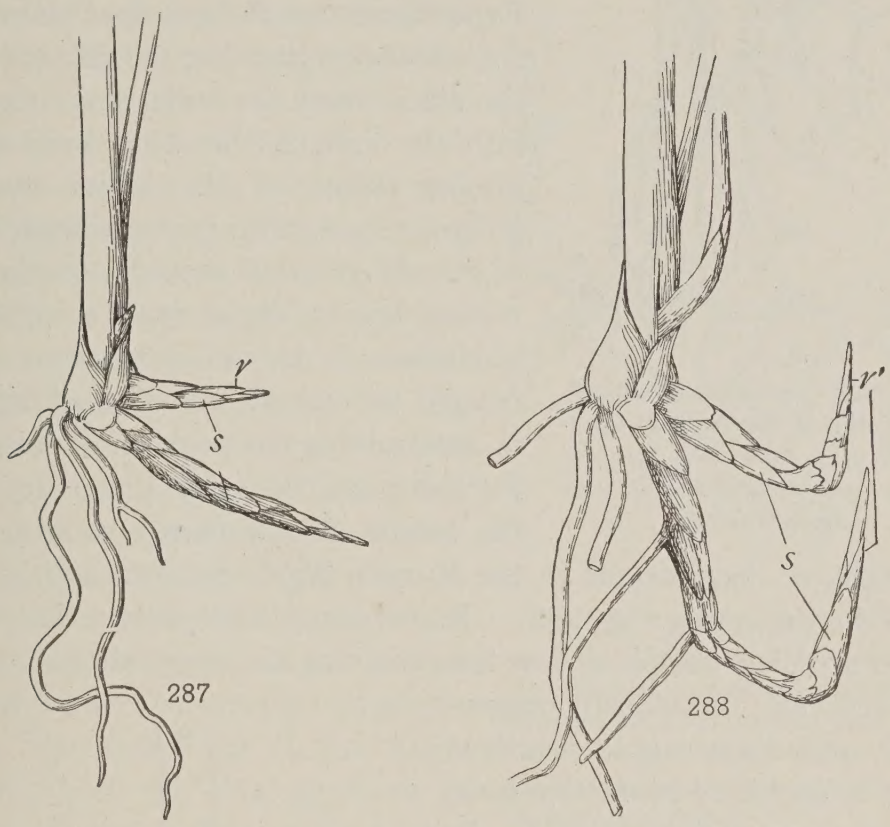


FIG. 286. — The horizontal underground stem (rhizome or rootstock) of a false Solomon's seal (*Smilacina stellata*); note the erect stalk of the current season (*e*) and the bud (*b*) which gives rise to a similar erect shoot the following season; note also the lateral branch (*b'*), the beginning of another potential plant; *r*, adventitious roots.

Rhizomes or rootstocks. — *General features.* — *Rhizomes* or *rootstocks* are horizontally elongated underground stems, which occasionally compose the entire stem system of the plant (as in various violets and in most ferns), but which more commonly give rise to erect annual stems that bear foliage leaves and flowers (fig. 286). In the latter case the rhizome bears only scale leaves (figs. 287, 288), in whose axils erect stems may originate, while in the former, foliage leaves and even flowers (as in some violets) issue directly from the rhizome. In some

species of *Viola* and *Polygala* underground flowers develop from rhizomes (fig. 497).

The reactions of rhizomes to changes of soil level. — The horizontality of rhizomes has led to the general conception that they are diageotropic organs, as probably is the case under ordinary conditions. However, rhizome activities are too complicated to be accounted for solely



FIGS. 287, 288. — Rhizomes of the cord grass (*Spartina cynosuroides*): 287, the basal portion of a shoot, as seen in summer, showing the origination of new rhizomes (*r*), which are completely ensheathed by overlapping scale leaves (*s*); 288, a similar shoot, as seen early in the following spring; note the sharp change in the growth direction of the rhizomes (*r'*) from progeotropic to apogeotropic.

by diageotropism. The underground stems of most species have a definite position in the soil, varying from a considerable depth, as in *Equisetum*, *Asparagus*, and many xerophytes, to a slight depth, as in *Juncus balticus* and many swamp plants and mesophytes. When a rhizomatous plant is transplanted, it grows up or down to its specific soil level, thenceforth growing horizontally. If soil is added, the rhizome begins to ascend, sometimes almost vertically, as when *Juncus balticus* is submerged by a dune (fig. 289); if soil is removed, the rhizome descends. Thus a rhizome grows parallel to the soil surface;

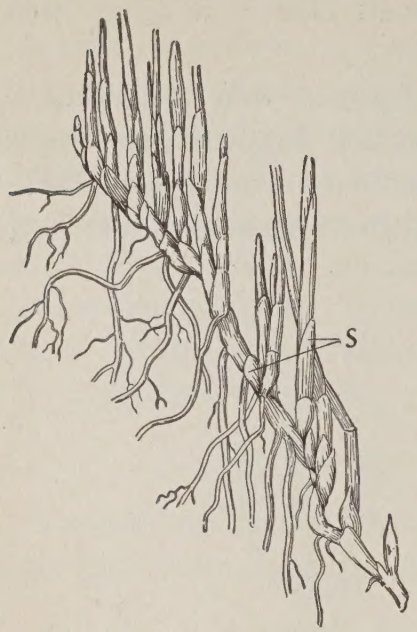


FIG. 289. — An obliquely ascending rhizome of *Juncus balticus*, illustrating the reaction of this species to sand submergence; *s*, scale leaves. — From SCHOLZ.

this phenomenon is known as maintenance of soil position and is said to illustrate the *law of level*. The cause of this extraordinary behavior is complex but it is believed that the nature of the geotropic reaction varies with the depth. Experiments on *Polygonatum* show that the distance separating the rhizome from the place where the aerial shoot emerges into the light is the chief depth-determining factor; if the aerial shoot is obliged to pass through a darkened layer of air, the rhizome ascends, precisely as if a soil layer of equal depth were added. Variations in the soil moisture or in the oxygen content of the soil also may aid in determining the position of rhizomes. Furthermore, behavior may vary with the season, stems often appearing progeotropic or diageotropic in the autumn (figs. 287, 290) and apogeotropic in the spring (fig. 288). Experiments have shown that many shoots are diageotropic at low temperatures and apogeotropic at high temperatures. Obviously, progeotropic and diageotropic reactions result in increased protection from transpiration and from cold. In *Circaea* and in *Solanum tuberosum*, the rhizome develops into an erect shoot, when the aerial stem is removed. This experiment appears to show that such rhizomes are apogeotropic organs whose customary horizontality is due to the inhibition of verticality by the erect stem, much as the growth directions of lateral stems and roots are due to the inhibition of verticality by the primary organs.

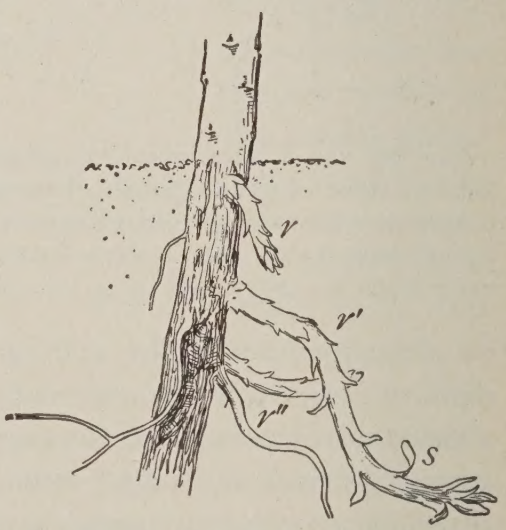


FIG. 290. — The basal portion of a shoot of the ditch stonecrop (*Penthorum sedoides*), showing the development of new rhizomes; note that the upper rhizomes (*r*, *r'*) are more pronouncedly progeotropic than are the lower rhizomes (*r''*); *s*, scale leaves.

Linear and radial migration. — In the simplest rhizomes, branching is comparatively slight, and each season there is a new growth of several centimeters at the anterior end, while at the posterior end a corresponding portion may decay. Thus the plant occupies a new position in the soil each year, and if the advance is in lines, as in *Polygonatum* and in *Juncus balticus*, the phenomenon is known as *linear migration.* In *Juncus* several erect shoots develop in a line each year, making linear migration very obvious, even to the casual observer. In Solomon's seal (*Polygonatum*, fig. 291) a single erect shoot develops each year, and, as it leaves a definite scar, it is possible to determine the age of the undecayed portion of the rhizome; it is possible also to learn something of the life conditions of each season on account of variations in the annual increment. More commonly the radiation and branching of rhizomes in all directions from the original center result when isolated in symmetrical colonies of ever increasing circumference. Sometimes (as in the flags) the death of the older portions in the interior of such a colony results in the formation of a ring, comparable to the "fairy rings" of various fungi (p. 322), though continued branching is more likely to keep the entire space occupied (fig. 292).

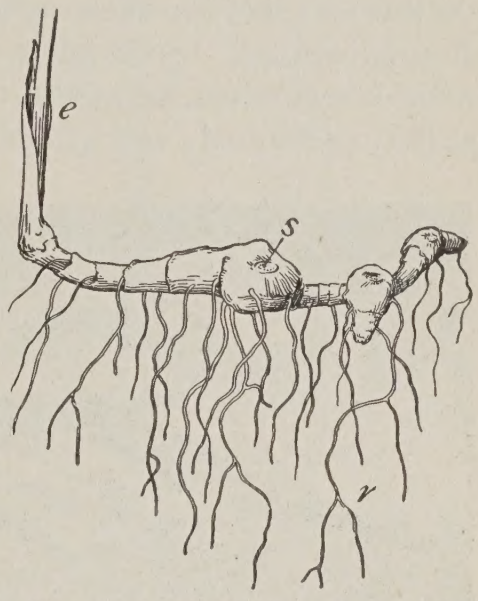


FIG. 291. — A rhizome of the Solomon's seal (*Polygonatum biflorum*); note the tuberous enlargements of the rhizome with the conspicuous scars (*s*) left by the fall of the erect stems of previous seasons; *r*, adventitious roots; *e*, erect stem of the current season.

The rôle of rhizomes. — The rhizome habit, perhaps more than any other, facilitates the occupation of space by plants, especially because adventitious roots and erect shoots develop at various points on the radiating stems. The older parts gradually decay, so that the branches become isolated as separate plants; consequently there is an increase in the number of individuals as well as in the space occupied. In this phenomenon of vegetative reproduction, however, it is not a matter of particular importance whether or not the actual number of individuals is increased by isolation. The important matter is the occupation of new space, for in any case a *rhizome colony* or rhizome complex repre-

sents a number of potential individuals, as is well shown after the plowing of a field partially occupied by such plants (*e.g.* the couch grass, *Agropyrum repens*); the rhizomes are dislodged and broken and the scattered fragments form new centers of migration.

The great advantage of rhizomes as organs of propagation is due partly to their horizontality, partly to their elongation, and partly to the fact that they are soil structures and thus are able to invade regions already occupied. Seeds fall in numbers everywhere, but hundreds die where one develops, because of the difficulty of striking root in ground already preëmpted; even plants with runners propagate with difficulty

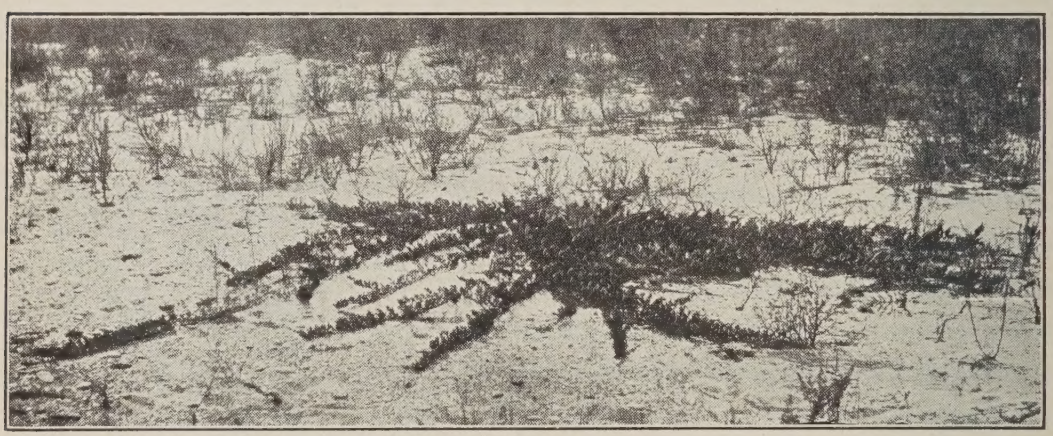


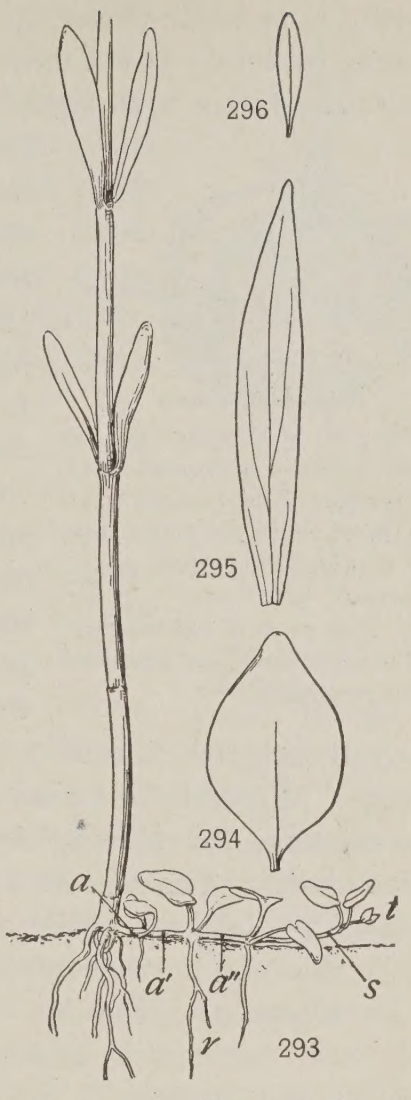
FIG. 292. — A plant of the creeping juniper (*Juniperus horizontalis*), illustrating radial migration; horizontal branches advance in all directions, rooting in the sand; in the background are numerous plants of *Artemisia;* Waukegan, Ill. — Photograph by MCCALLUM.

where vegetation is dense. Rhizomes, however, penetrate the soil of forests or of grasslands scarcely less readily than that of open grounds. The advantage of the rhizome habit is well illustrated in fields that have lain fallow; during the first year, annuals usually dominate, but little by little rhizome plants and other perennials increase their area, invading the space previously occupied by annuals, until finally all of the latter are excluded.

Often it is thought that plants exhaust the soil in which they grow, and therefore that rhizomes are additionally advantageous in that the plant has a means of migrating into new soil richer in food materials. However, it is now known that plants rarely exhaust the soil, at least in nature. It might be supposed that migration is advantageous as a means of withdrawal from soil regions in which deleterious root excretions have accumulated, but the persistent occupation of the same spot makes this view rather untenable, except, possibly, for those rhizomes or rhizome colonies (*e.g.* in *Polygonatum*) which migrate as a whole into new areas; this consideration weighs equally against the soil exhaustion theory. Maintenance of soil

level probably is advantageous, since great depth interferes with the development of aerial organs, while extreme shallowness would mean lessened soil protection and greater difficulty in the invasion of new areas, because of the increasing occupation of space toward the surface. Rhizomes are advantageous further as organs of persistence through unfavorable seasons (p. 231) and as organs of food accumulation; in *Psilotum* and in *Corallorhiza* they replace roots, and even may bear "root hairs."

Runners. — *General features.* — *Runners* are horizontal stems at or above the ground level, taking root in the soil, and differing from rhizomes chiefly in not being subterranean. *Stolons* are essentially identical with runners, though the term sometimes is applied to certain rhizomes. Runners usually are much slenderer than rhizomes, and often their internodes are greatly elongated; chlorophyll commonly is present. If runners come into contact with moist soil, roots and buds develop at the nodes, thus giving rise to potential or actual new plants (fig. 293). A representative runner is that of the strawberry in which there is a continuation of horizontal elongation accompanied by repeated rooting, thus giving rise to a number of potential plants. Sometimes (as in *Sempervivum* and *Saxifraga*) the runner ceases to elongate after a bud has developed; in such cases the term *offset* may be used (fig. 471). Creeping



FIGS. 293–296. — *Satureja glabra:* 293, the basal portion of a plant, showing a runner (*s*) in which all of the leaves appear to issue from the upper side, because of stem twisting and petiole curvature; at the nodes adventitious roots (*r*) issue from the under side of the runner, fastening it to the ground; note the unfastened ascending tip (*t*); if the runner is severed at *a*, *a'*, or *a''*, the rooted portions develop into independent plants; 294, a short, broad leaf, characteristic of a runner, developed especially in the autumn, and remaining over winter; 295, an elongated, narrow leaf, characteristic of the erect stem; 296, a short, narrow leaf, characteristic of the floral region; 294–296 equally magnified.

stems (as in white clover) are runners which lie close to the ground, rooting copiously at the frequent nodes (fig. 13). Also to be classed with runners are such stems as those of *Decodon* and *Rubus* which bend over and take root if the tip comes into contact with moist soil. *Prostrate stems* differ from runners in not taking root, though stems classed as prostrate (*Arctostaphylos*, *Juniperus horizontalis*, fig. 292) frequently develop roots under favorable conditions. When the stems of *Decodon* or *Rubus* bend over and root at the tip, probably it is because there is not sufficient mechanical tissue to hold the stems erect. Possibly the same is true of many runners, since they often appear prophototropic at the outset. In any case, the development of adventitious roots is likely thenceforth to cause a downward pull on the older parts of the runner. *Nephrolepis* is somewhat unique in possessing both rhizomes and runners; the rhizomes develop first and give rise freely to adventitious roots. The runners are peculiar leafless organs without a conspicuous rôle; if they are removed, some of the rhizomes develop into aerial shoots.

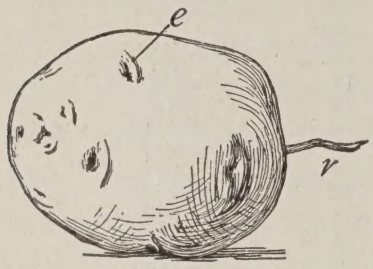


FIG. 297. — A tuber of the potato (*Solanum tuberosum*); note the remains of the rhizome (*r*) at the end of which the tuber grew and of which it is merely an enlargement; the "eyes" (*e*) are buds, some or all of which sprout and develop into stems, when the tuber germinates.

The advantages of runners. — Runners compare favorably with rhizomes as organs of vegetative reproduction, as may be seen in the development of a colony of strawberries or of white clover. They commonly elongate more than do rhizomes, possibly because the medium in which they grow offers less resistance; such elongation favors more rapid migration and the development of new individuals at a greater distance from the old. Creeping stems appear to be almost as advantageous as

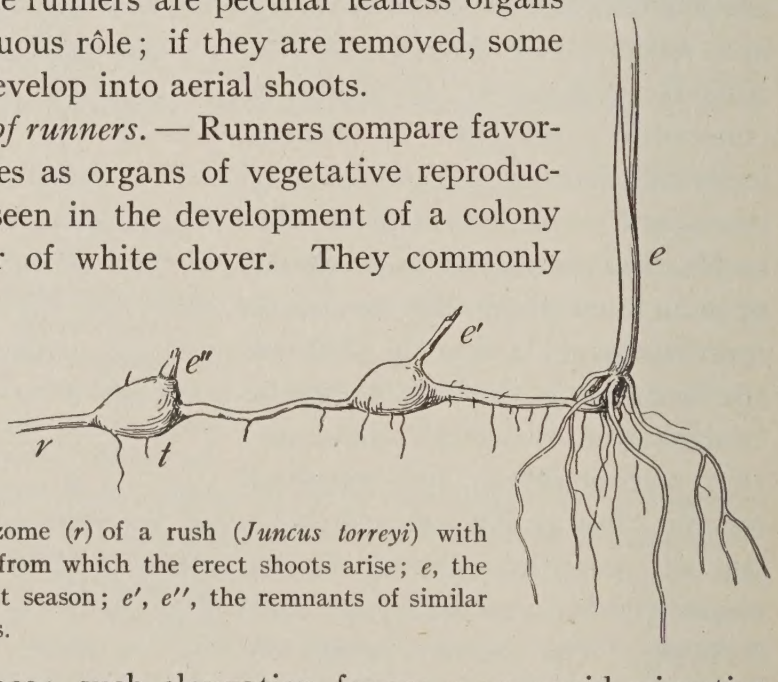


FIG. 298. — The rhizome (*r*) of a rush (*Juncus torreyi*) with tuberized portions (*t*), from which the erect shoots arise; *e*, the erect stem of the current season; *e'*, *e''*, the remnants of similar shoots of former seasons.

rhizomes, since they grow close to the ground in a position favorable for the development of the adventitious roots that are necessary for propagation. In *Decodon* and *Rubus*, and even in the strawberry, it is much more difficult for the stems to come into contact with the ground. While most creeping stems remain alive for some years, as do rhizomes, the internodes of strawberry runners soon die, so that the new potential plants soon become actual individuals.

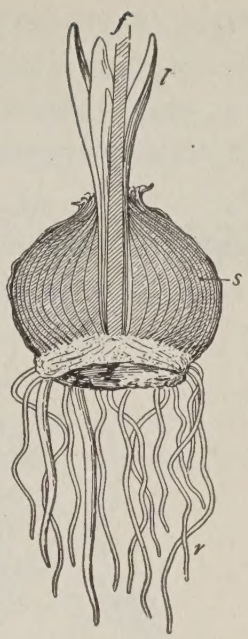


FIG. 299.— A median longitudinal section through the bulb of a hyacinth (*Hyacinthus orientalis*), showing the overlapping scale leaves (*s*) which compose the bulb; the innermost leaf primordia develop into foliage leaves (*l*); *f*, flower stalk; (*r*), adventitious roots.

Tubers, bulbs, and corms. — *Tubers.* — A *tuber* is essentially a rhizome in which elongation is replaced by stem enlargement, as in the potato, in which the underground stem begins as a rhizome, but later develops at the growing tip into a tuber (fig. 297). In *Scutellaria parvula* and in *Juncus torreyi* the rhizome alternately elongates and enlarges, thus developing a beadlike (moniliform) chain of tubers (figs. 298, 291, 376). In nature each tuber usually gives rise to an erect shoot, forming one potential plant; or an actual plant may result, if the rhizome portions die, as in the potato. As a matter of fact, tubers represent at least as many potential plants as there are buds or "eyes," potato tubers commonly being cut into several pieces for planting. Even in tuber fragments without "eyes" a bud may organize and grow into a plant. In one of the yams (*Dioscorea sativa*), there are aerial tubers, which are of importance in reproduction.

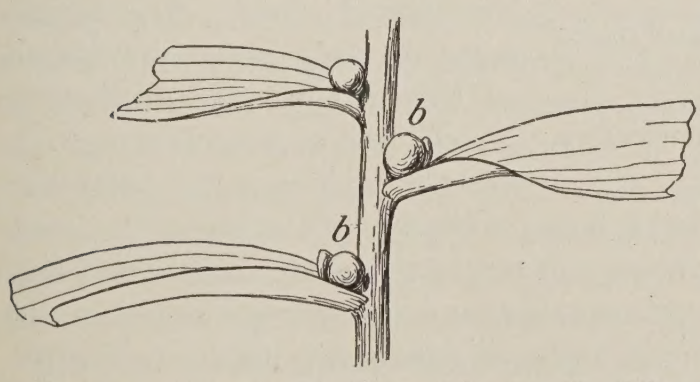


FIG. 300. — A portion of a shoot of the tiger lily (*Lilium tigrinum*), showing the bulbils (*b*) which develop in the axils of sessile foliage leaves; these bulbils readily become detached and fall to the ground.

Bulbs. — *Bulbs* are underground stems differing from tubers and rhizomes in their almost total lack of stem elongation, and in the fact that the

main axis is vertical and is enclosed by a number of relatively large overlapping scale leaves in which food accumulates (as in the lilies, fig. 299). Sometimes, as in the tiger lily (fig. 300) and in *Lycopodium*, bulbs develop on aerial stems; in some species of *Sedum*, ordinary axillary buds drop off and develop into independent plants. Bulbs usually give rise to a single potential plant.

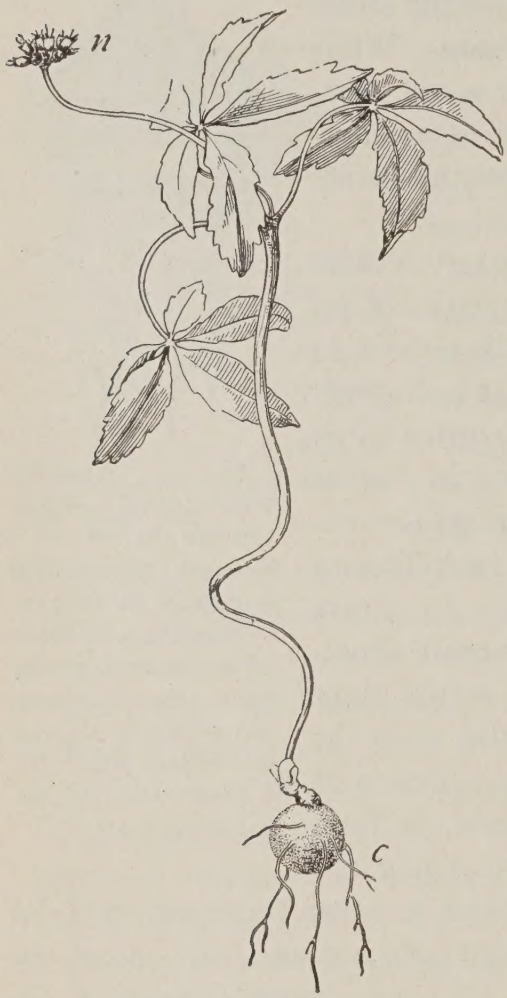


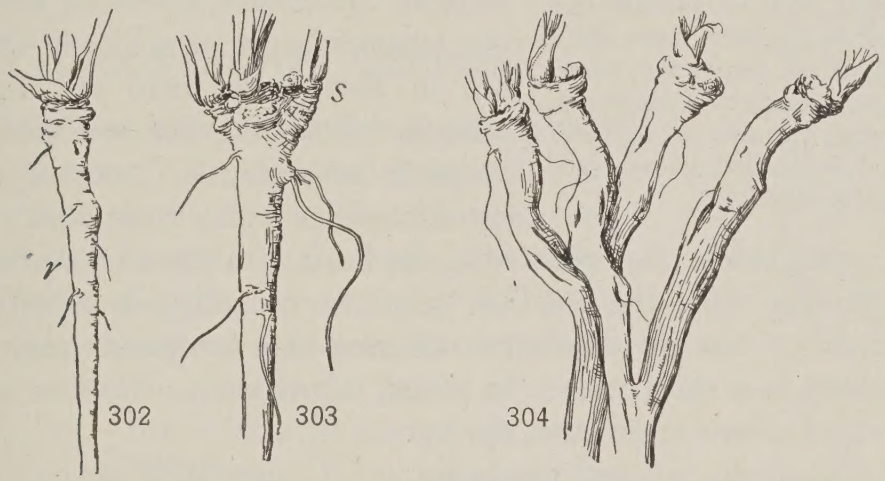
FIG. 301. — A plant of the dwarf ginseng (*Panax trifolium*), showing a corm or solid bulb (*c*); note the whorl of three palmately compound leaves and the umbel of pistillate flowers (*n*).

Corms. — *Corms* usually agree with bulbs in having vertical orientation, slight stem elongation, and prominent apical buds, while they agree with tubers in their inconspicuous scale leaves and in the accumulation of food in the stem (fig. 301). Transitions exist between the various kinds of underground stems, for example, in *Trillium*.

The advantages of tubers, corms, and bulbs. — Tubers, corms, and bulbs are much inferior to rhizomes and runners as propagative organs, particularly because their slight elongation limits the number of potential plants developed and permits but slight migration from the original center. The advantages of these organs are found rather in food accumulation (p. 234) and in protection (p. 231). When a tuber (as in the potato) or a bulb (as in *Erythronium*) is borne at the end of a rhizome, the possibilities of effective migration and reproduction are unsurpassed, but this is due chiefly to the rhizome element in the underground stem, the tuberous or bulbous portion being of significance mainly in furnishing an abundant supply of food to the new plant. Tubers, corms, and bulbs, like rhizomes, have a definite soil level varying with the species, the largest forms commonly having the greatest depth. Be-

cause of their slight migratory powers it takes these organs much longer than rhizomes to reach the proper level when displaced; however, in such forms as *Erythronium* the rhizomes (sometimes called *droppers*) which bear the new bulbs grow up or down as the case may be, placing the new plant at the proper level (figs. 19, 20). In *Erythronium albidum* there has been recorded a descent of ten centimeters in one season. The soil position of tubers, corms, and bulbs is believed to depend chiefly upon their distance from the synthetic organs, and to a smaller degree upon variations in soil moisture.

Reproduction by stems in water plants. — *General features.* — Aquatics rooted in the soil reproduce by underground stems and runners



FIGS. 302–304. — Multicipital stems in the dandelion (*Taraxacum officinale*): 302, a young plant, showing a simple tap root (*r*) crowned with a single rosette of leaves; 303, an older plant, showing a larger root, crowned with a multicipital stem (*s*) with three leaf rosettes; 304, a much older plant, showing how a dandelion plant eventually may break up into several individuals.

exactly as do land plants, except that migration usually is more rapid, perhaps because of the easy penetration of the oozy slime at the bottom of ponds. Some rhizomatous plants (as *Hippuris*, *Limnanthemum*, and species of *Potamogeton*) may advance as much as a meter a year, soon filling a small pond (fig. 471). The water lilies have gigantic rhizomes in which considerable surplus food accumulates; the rhizomes of bulrushes, cattails, and flags, though much smaller, are large as compared with most rhizomes, yet they migrate with some rapidity.

The remarkable capacity of water plants for vegetative reproduction is due chiefly to the ready detachability of aquatic stems, whose fragments float to a more or less distant locality, where a new growth center is established. A striking case of vegetative reproduction among

hydrophytes is seen in *Eichhornia* (the water hyacinth), which in recent years has filled various streams in Florida to such an extent as to impede navigation; another remarkable example is afforded by *Elodea canadensis* (often called the water pest, because of its rapid filling of ponds), which, from a single plant introduced from America, spread over Europe within half a century; this rapid spread probably was due entirely to vegetative reproduction, since only pistillate plants of *Elodea* are known in Europe. In *Elodea*, spreading is due to the fragmentation of ordinary shoots, but in *Eichhornia* there are aquatic runners which give rise to readily detachable new plants. Another rapid spreader is the water cress, which soon fills a spring brook when planted at the head. In the duckweeds new thalli develop from the old (figs. 305, 28), becoming detached with such rapidity that the vegetative offspring of a few plants may fill a small pond in a short time. In rivers, migration is, of course, much more rapid downstream than up, yet water plants may advance upstream, and even may migrate from one river or pond to another; wind and fish may be agents of dispersal upstream, and it is the current belief that the feet of wading birds are important agents in carrying plant fragments from one pond to another. Clearly the culmination of vegetative reproduction among seed plants is to be seen in fragmenting hydrophytes, where stem detachability facilitates dispersal as much as does seed production.

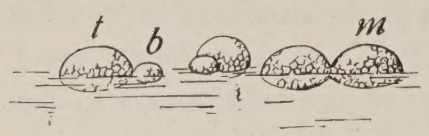
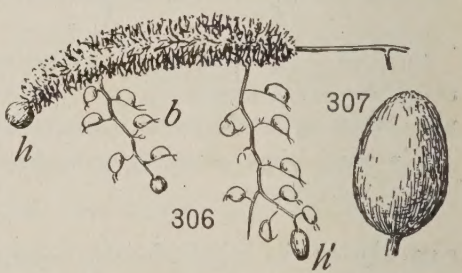


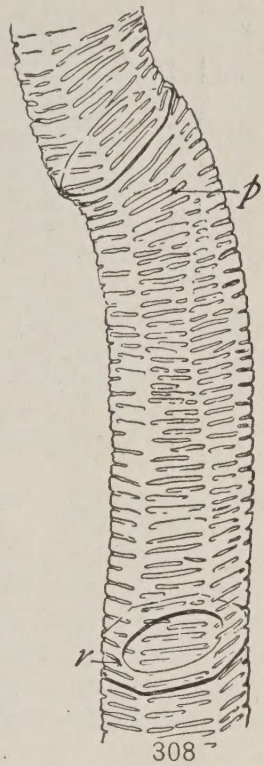
FIG. 305. — Plants of one of the smallest of the duckweeds (*Wolffia*), whose body is reduced to a thallus (*t*); note that vegetative reproduction occurs through the development of a bud (*b*), which becomes detached at maturity, as at *m*; note also that a part of the thallus is below and a part above the water, the former having to do chiefly with the absorption of water and salts and the latter with food-making and transpiration; considerably magnified.



FIGS. 306, 307. — Winter buds (hibernacula) of the bladderwort (*Utricularia*): 306, a portion of a shoot of the land form of *Utricularia intermedia*, showing a horizontal axis, terminating in a winter bud (*h*); note also that the progeotropic earth shoots have terminal winter buds (*h'*) and conspicuous bladders (*b*); 307, a winter bud of *Utricularia vulgaris*. — From GLÜCK.

Winter buds. — In many aquatics there develop special *winter buds* or *hibernacula*, which readily become detached and drop to the bottom of the pond because they are heavier than water. In the duckweeds this heaviness is due to the relative

lack of air spaces, while in *Utricularia*, it is due to the compact growth of either the terminal or the lateral buds, the stem ceasing to elongate and the leaves being very closely imbricated; the whole forms a somewhat globular structure (figs. 306, 307). In spring most hibernacula develop roots, and the stem elongates into an ordinary vegetative shoot; however, in the duckweeds and in *Utricularia*, soil roots do not appear, and the developing plants soon become lighter than water and rise to the surface. In *Utricularia*, winter buds may be induced experimentally at any season. The chief advantage of hibernacula is the preservation of the species over inclement seasons; however, they represent new plants that have arisen vegetatively from the parent individual and thus are reproductive structures.



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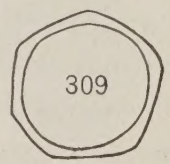

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FIGS. 308, 309. — A portion of a scalariform vessel (trachea) from the root of the prickly lettuce (*Lactuca scariola*): 308, a longitudinal view showing how tracheae arise from tracheids through the resorption of the cross walls; note that these walls have been resorbed except for rings of tissue (*r*) next to the longitudinal walls; note also the transversely elongated pits (*p*), characteristic of scalariform vessels; 309, a cross section of such a scalariform vessel; both figures highly magnified.

3. CONDUCTIVE TISSUES

General remarks. — Water and solutes may move from any cell to any adjoining cell, if the walls are permeable to the diffusing substances. In most small plants special conductive tissues are absent; also they are absent or poorly developed in submersed aquatics, where the food-making organs are likewise organs of water absorption. But in all large land plants, where the organs of synthesis are remote from the organs of absorption, *conductive tissues* are well developed. The substances that migrate from cell to cell are either raw materials (water and inorganic salts) or organic foods commonly manufactured by the plants themselves, water being quantitatively much the most important migrating substance. These materials move from regions of higher to regions of lower pressure, water and soil salts ascending from the roots to the leaves, and organic foods moving in various directions from the seat of manufacture in the leaf.

The structure of the conductive elements. — *Tracheids and tracheae.* — When conductive cells begin to differentiate from other cells, their chief distinctive feature is elongation,

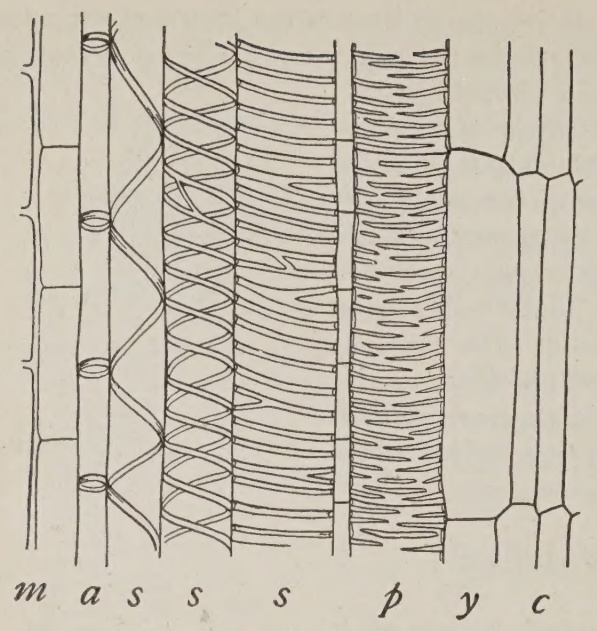


FIG. 310. — A diagrammatic longitudinal section of a young xylem strand; *c*, cambium; *y*, a young undifferentiated trachea with cross walls as yet unresorbed; *p*, a trachea with transversely elongated pits; *s*, spiral tracheae; *a*, an annular trachea; *m*, pith; highly magnified. — From BARNES (Vol. Two).

which remains the most fundamental characteristic common to all conductive elements. The commonest conductive elements are *tracheae* (also called *vessels* or *ducts*) and *tracheids*, which together are sometimes called *hydroids*, a term suggestive of their rôle in water conduction. Tracheids arise through the differentiation of certain parenchyma cells which elongate and enlarge, the walls also becoming *lignified* (*i.e.* woody); at maturity they commonly are *prosenchymatous*, that is, their ends are pointed, owing to the development of oblique walls from originally transverse terminal walls (figs. 213, 243). Tracheae differ from tracheids in being cell fusions or *syncytes*, arising through the resorption of the end walls. Thus a tracheid may represent only a stage in the development of a trachea, as in young angiosperm tissue, all transitions sometimes being observed (figs. 308–310). However, in ferns and conifers and in the bundle termini of angiosperm leaves, tracheids usually remain as such, that is, the end walls are not resorbed (fig. 311).

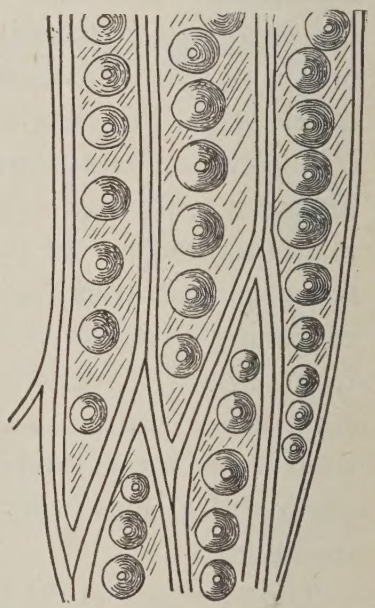
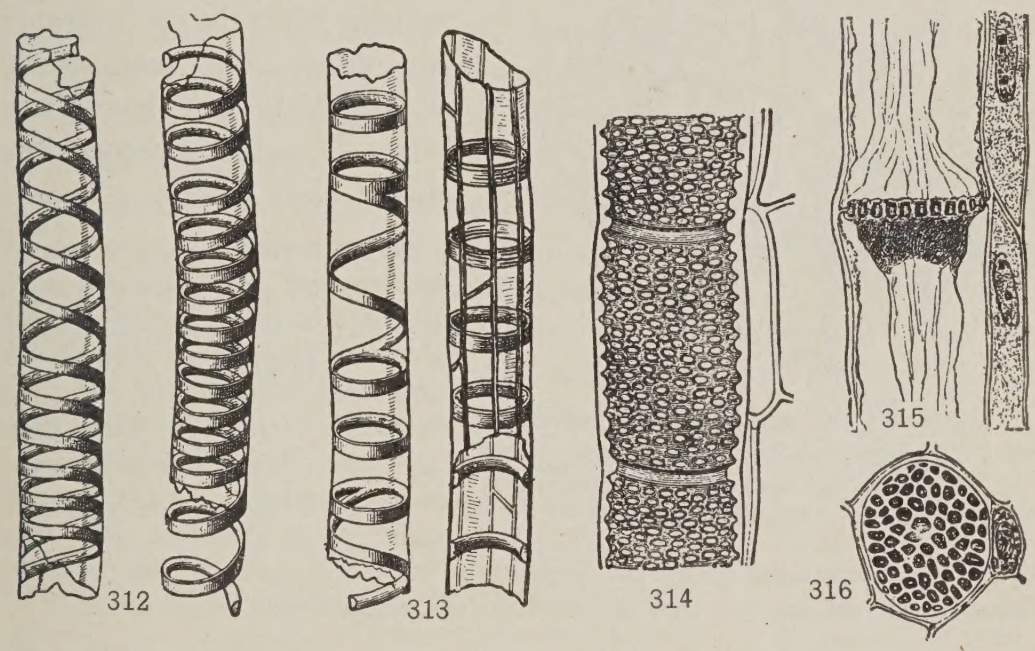


FIG. 311. — Tracheids of a gymnosperm with bordered pits; highly magnified. — After CHAMBERLAIN.

Tracheids are much shorter than tracheae, rarely exceeding a millimeter in length, though sometimes attaining a length of twelve centimeters (as in *Nelumbo*) or even a meter (as in some conifers). Tracheae rarely are longer than ten centimeters, though they may attain a length of one or two meters in *Quercus* and three to six meters in lianas

(as *Wistaria*) and in *Eucalyptus*. While isolated tracheids and tracheae sometimes occur, they usually are grouped in continuous strands traversing the entire plant body.

Individual tracheids or tracheae, even within a single conductive strand, vary widely in wall sculpturing, owing to differential lignification. When the thickenings are *annular* or *spiral*, the wall area largely remains thin (figs. 310, 312, 313). In *reticulated* vessels, the strengthening fibers form a network, and in the *pitted* tracheids and tracheae, most of the wall becomes thickened, the thin places appearing as small pits (fig. 314). Pitted and reticulated vessels usually are larger than those with annular or spiral thickenings. Still another form of thickening is seen in the



FIGS. 312–316. — Vascular elements of an angiosperm: 312, spiral vessels; 313, spiral and annular vessels; 314, a pitted vessel; 315, a sieve tube with companion cells; 316, a cross section of a sieve tube at the sieve plate, showing also a companion cell in cross section; 312–315, are from longitudinal sections; all figures highly magnified. — 312 and 313 after BONNIER and LECLERC DU SABLON; 314 after DEBARY; 315 and 316 after STRASBURGER.

scalariform vessels, in which transversely elongated pits occur in parallel rows (fig. 308). *Bordered pits* occur in many plants, especially in the conifers, where they are arranged in longitudinal rows, a surface view disclosing two concentric rings or ellipses (fig. 311); in section there are seen a thickened central portion, the *torus*, and a thin margin, the *margo*, the latter representing the space between the rings as seen in surface view. When the thickening of tracheids and tracheae is completed, the cell contents die, after which the lumen contains water and solutes, together with numerous air bubbles. In old wood the lumina contain largely air, although various excreted products often accumulate.

Sieve tubes and conductive parenchyma. — *Sieve tubes* are syncytes, occurring in continuous rows, like tracheae, but differing therefrom in

their thin cellulose walls and in their living and highly albuminous viscous contents (fig. 315). They rarely exceed two millimeters in length, in this respect resembling tracheids rather than tracheae. A unique feature of sieve tubes, giving rise to their name, is the presence at their widest parts of perforated oblique or transverse *sieve plates*, which sometimes occur also on the side walls (figs. 316, 317). The sieve plates may be enwrapped by a highly refrangible *callus*, which is easily soluble, disappearing when the cell contents are dilute, but reappearing and closing the sieve plate when the contents become less dilute, as in winter.

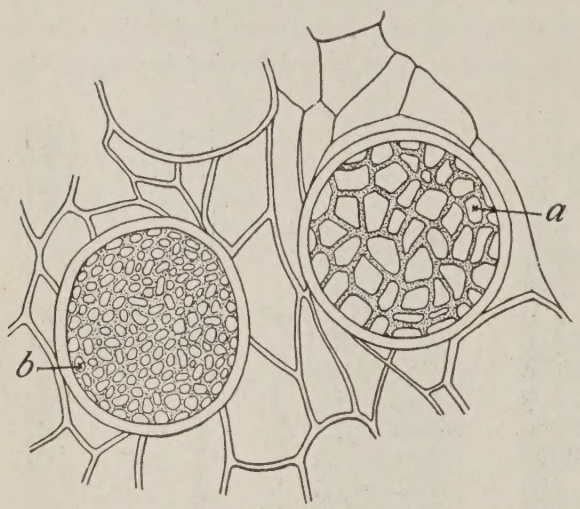


FIG. 317. — Cross sections of sieve tubes of a gourd (*Lagenaria vulgaris*), showing sieve plates with large pores (*a*) and with small pores (*b*); highly magnified. — From DEBARY.

In angiosperms sieve tubes are accompanied by *companion cells*, elements of smaller caliber, whose abundant cytoplasmic contents are connected prominently with the cytoplasm of the sieve tubes (figs. 315, 316). Besides specialized elements, conductive areas contain many parenchymatous cells that remain undifferentiated except for elongation; such cells make up the so-called *conductive parenchyma*, but they do not differ essentially from cortical cells.

Primary conductive tissues. — *The arrangement of conductive elements into strands or bundles.* — Sometimes tracheids occur as isolated cells or *idioblasts* (as in *Salicornia*, fig. 73), but in such cases they are not to be regarded as conductive cells. Sometimes there are simple strands, such as isolated bundles of sieve tubes and the finer leaf veins, which are composed chiefly of tracheids. But in most cases all the conductive elements are grouped into *compound bundles*, notably in the ferns and seed plants, although suggestions of conductive bundles as well as of conductive cells are found in many non-vascular plants. A strand made up of conductive elements is known as a *vascular bundle* or as *mestome;* mechanical elements usually are closely associated with the conductive elements, the two making up a *fibrovascular bundle.*

Xylem and phloem. — Usually there are two more or less distinct regions within the bundle, namely, the *xylem* which contains tracheae or tracheids, and the *phloem* which contains sieve tubes and their asso-

ciated elements (fig. 61). Sometimes xylem and phloem are indistinguishable from one another, as in certain hydrophytes. Both phloem and xylem may contain mechanical elements, and just as the conductive elements as a whole are known as the mestome, so the mechanical elements as a whole, either within or without the fibrovascular bundle, are known as the *stereome*. The conductive portion of the xylem is known as *hadrome* (or *hydrome*), and the conductive portion of the phloem is known as *leptome;* for example, phloem may contain such stereome elements as bast fibers and such leptome elements as sieve tubes, while secondary xylem may contain such stereome elements as wood fibers and such hadrome elements as tracheae or tracheids.

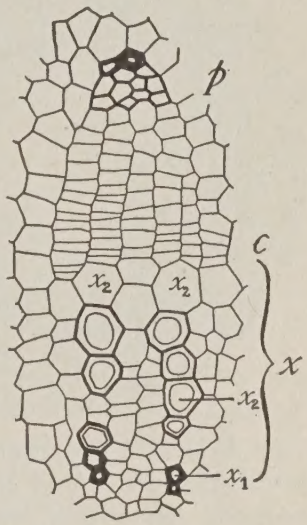


FIG. 318. — A cross section of a vascular bundle in which secondary thickening is in progress; *p*, phloem; *c*, cambium from which secondary phloem and xylem are forming; *x*, xylem, composed of primary xylem (x_1) and secondary xylem, (x_2); highly magnified. — From BARNES.

Secondary conductive tissues. — *The cambium ring.* — Soon after the formation of the primary vascular tissues, renewed growth takes place, especially in conifers and dicotyls; this results in the formation of *secondary tissues*, the active element in their formation being the *cambium*, a layer of cells that retain a capacity for active growth and hence known as meristematic (fig. 318). In addition to the *fascicular cambium*, representing the meristematic progeny of the *procambium* from which the primary xylem and phloem were developed, there is an *interfascicular cambium* which develops in the rays between the primary bundles. The most active division of the cambium cells is tangential, the new cells arising inward developing into *secondary xylem*, and those arising outward into *secondary phloem*. Radial division also takes place, resulting in the merging of the fascicular and interfascicular cambium into the *cambium ring*, whose circumference is subject to constant enlargement, owing to the outward growth of the secondary xylem cells, and to the tangential growth of the ring itself. This circumferential enlargement is responsible for the continued rupture and exfoliation of the bark.

Mature secondary tissues. — Secondary xylem remains as permanent tissue in shrubs and trees, thus bringing about an annual increase in diameter; secondary phloem is relatively ephemeral, being subject to

yearly renewal within and exfoliation without. An old tree has thicker bark than a young tree, partly because each year the new secondary phloem a little more than offsets the amount exfoliated, and partly because of the activity of the phellogen (p. 220). As in primary tissues, the phloem is made up of sieve tubes, companion cells, parenchyma, and mechanical elements (mostly bast fibers), while secondary xylem consists of tracheids or tracheae, parenchyma, and characteristic mechanical elements known as wood fibers; all gradations exist between these fibers and ordinary tracheids or tracheae. Rays of parenchymatic cells, the *medullary rays*, traverse the secondary tissue radially (fig. 319). In woody monocotyls and lianas secondary growth diverges considerably from that just described. In the secondary wood the tracheids and tracheae soon die, though much of the parenchyma remains alive for some years. The living portion of the wood is known as *sapwood* or *alburnum*, while the dead portion is known as *heartwood* or *duramen*. Usually the alburnum and duramen differ in color and otherwise, owing to the accumulation of excreta in the latter.

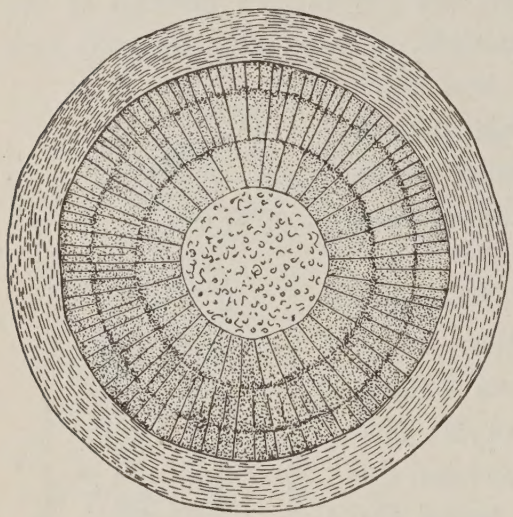
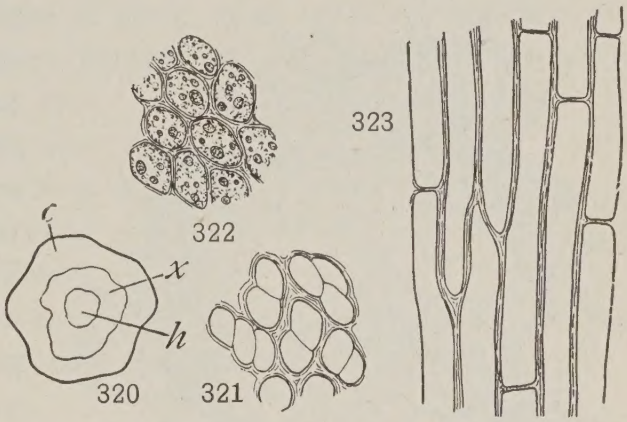


FIG. 319. — A diagrammatic cross section of the stem of a dicotyl, the box elder (*Acer negundo*), illustrating secondary growth; there are shown three annual growth rings of xylem formed from the cambium; inside of the first ring is pith; the lines traversing the growth rings represent medullary rays and the outer layer represents the bark. — From COULTER (Vol. One).

Conductive cells and tissues in non-vascular plants. — *Thallophytes and liverworts.* — In vascular plants the first step in the development of conductive cells from parenchyma is elongation in the direction of maximum conduction. In many lower plants similarly elongated cells more or less grouped into tissues are by no means infrequent (as in the stipes of the larger fungi). Many fungi have elongated rootlike organs which conduct foods for long distances. Much the most remarkable conductive system in thallophytes, however, is that in the brown and the red algae, where in the larger species there are central strands of elongated cells with viscous albuminous contents and with transverse sieve plates at the widest portions, resembling those found in the leptome of seed plants; there is also a characteristic callus. Tracheids do not occur in the algae, but water plants in general have a better development of sieve tubes than of tracheids or tracheae. In liverworts there is but a slight suggestion of conductive tissues, though *Porella* exhibits elongated

cells, and the thallus of *Pallavicinia* contains a distinct midrib composed of elongated and pitted cells.

Mosses. — In the mosses elongated cells are frequent, especially in the stems, though they occur also in the midribs of many leaves. In the stem of the Polytrichaceae the structural differentiation approaches that found in ferns, the elements having a concentric arrangement; the central region consists largely of thick-walled cells, which, like tracheids, are prosenchymatous dead cells containing air and water (figs. 320–323). Often two or more of these central tracheid-like cells are associated in a group with a common thick wall, while the walls between the individual cells remain thin, suggesting an approach toward lateral fusion (fig. 321). This central xylem-like tissue is surrounded by a cylinder of living cells with albuminous contents (fig. 322). The underground stem or "rhizome" of the Polytrichaceae possesses a suberized "endodermis," a "pericycle," and a radial triarch arrangement of the "xylem" and "phloem," as in a triarch root. In the Polytrichaceae the leaf and stem bundles join, though they are not connected in most mosses. The bundle of *Polytrichum* certainly is more complex in structure than that of the simpler seed plants. The "vascular bundles" of algae and mosses doubtless have no genetic connection with the vascular bundles of higher plants, but they are of great interest as showing possible early steps in the differentiation of conductive tracts.



FIGS. 320–323. — The "vascular strand" of the leafy stem of a moss, *Polytrichum:* 320, a diagram, showing the stem regions, as seen in cross section; *c*, cortical region; *x*, leptome-like cylinder surrounding the central hadrome-like strand (*h*); 321, cells from the hadrome-like central strand; note that there are groups of thin-walled cells, suggesting lateral fusion; 322, cells from the leptome-like cylinder; note the abundant cell contents; 323, a longitudinal section through a part of the central strand, showing elongated prosenchymatic cells; all figures highly magnified.

Variations in primary conductive tissues due to external factors. — *General remarks.* — The vascular system often has been regarded as essentially invariable, so far as external conditions are concerned. Many investigations, however, show that vascular tissues react to external changes quite as do other tissues, variations being brought about readily, not alone in the shape, size, and number of the cells or cell fusions, but also in the position of the vascular tract and in the arrangement of its members. It is possible in certain cases even to inhibit the development of entire vascular strands, or to stimulate the appearance of others in unusual positions. Contrary to earlier views,

internal tissues appear to react to external changes about as readily as do such external tissues as the epidermis.

Water and vascular development. — In amphibious plants different individuals of the same species, or even different parts of the same plant, display more extensive and more specialized conductive tissue in organs exposed to transpiration than in similar organs that are submersed. Similarly, in land plants of a given species the conductive tracts are much better developed in dry air or dry soil than in moist air or moist soil. Thus desiccation, whether brought about by increased transpiration or by diminished absorption, appears to stimulate increased vascular development. In dry cultures the vessels are more numerous, larger, longer, and have thicker walls than in moist cultures; some of the smaller veins present in the dry cultures are absent in the moist cultures, remaining as undifferentiated parenchyma. Furthermore, in the drier cultures lignification begins earlier and is much more pronounced, and the differential thickening of the walls is more conspicuous; also the endodermis, which often retains its cellulose walls in water or in moist air, has thicker and more completely suberized walls. Finally, the hadrome elements die much sooner in dry than in moist cultures. Where growth and transpiration are pronounced from the outset (as in bulbous plants), the first new vessels often are larger than where growth is slow (as in many seedlings).

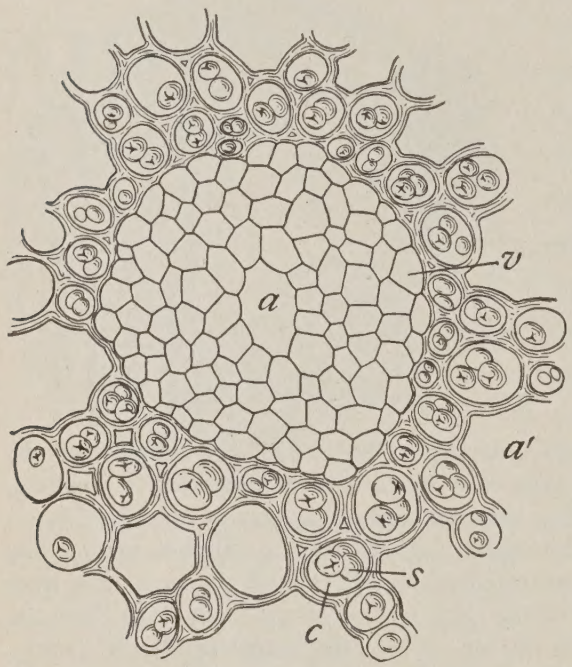


FIG. 324. — A cross section through the vascular bundle of a stem of the waterweed (*Elodea canadensis*); note that the vascular tract (*v*) is not obviously differentiated into leptome and hadrome, and that the vascular cells have thinner walls than the cortical cells (*c*); *s*, starch grains; *a*, intercellular air chamber within the vascular tract; *a'*, similar chambers in the cortex; highly magnified.

Observation tends to confirm experiment regarding the influence of water upon vascular development. In submersed hydrophytes, such as *Elodea* and *Ceratophyllum*, the vascular elements occupy a much

smaller space and are much less differentiated than in land plants of similar size, the leaf bundles often being so small as easily to escape detection (figs. 324, 325). Although the duckweeds are regarded as vascular plants, their conductive tissues are much less developed than are those of mosses like *Polytrichum*, entire organs sometimes having no vascular tissue, as in the roots of *Lemna*. In hydrophytes the leptome generally is reduced less than the hadrome, though in rare cases there may be but a single row of sieve tubes within a bundle. In contrast to hydrophytes, most xerophytes and alpine plants have highly developed conductive systems with large thick-walled elements, and an endodermis that is strongly suberized. Branch veins and veinlets usually are much more numerous in xerophytic leaves than in the leaves of shade plants and hydrophytes.

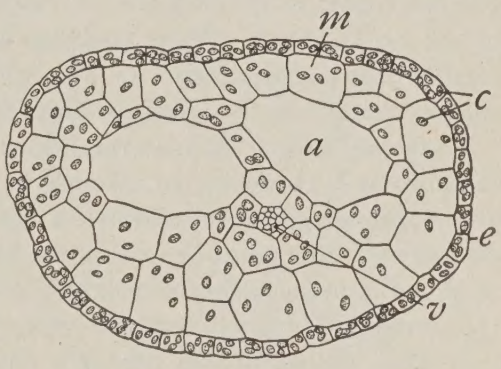


FIG. 325. — A cross section of a leaf segment of the hornwort (*Ceratophyllum demersum*), showing an extremely simple conductive bundle (*v*), made up of small undifferentiated cells; note the capacious air chambers (*a*) and the mesophyll (*m*), composed of nearly uniform cells which contain scattered chloroplasts (*c*), while the epidermis (*e*) contains densely packed chloroplasts; highly magnified.

Parasitism and vascular development. — When *Orobanche fasciculata* grows parasitically on an *Artemisia* root (fig. 390), the latter often is stimulated to unusual development, the hadrome in particular being subject to extensive enlargement. In the haustoria of *Melampyrum*, tracheids develop only after attachment to a host plant.[1] Leaves infested by the parasitic fungus, *Peronospora*, sometimes develop entirely new bundle tracts, certain primordia that commonly grow into mesophyll developing instead into vascular tissue. In insect galls of *Vitis* (fig. 129) there is a vast increase in hadrome, there being about the larval chamber a festoon of this tissue developed from the cortex. Sometimes in vascular tracts infested by parasites, parenchyma cells adjoining the enlarged vessels become hypertrophied, bulging out into the vessels as tyloses (p. 211).

Miscellaneous reactions of vascular tissue. — A potato tuber usually decays after giving rise to new tubers or rhizomes, which withdraw the food it had accumulated. But if a tuber is planted at the ground level in such a way that sprouts developing in the air are connected with the developing roots only through the old tuber (fig. 353), the latter not only lives another season, but many of its mature cells become once more meristematic. Among such rejuvenating tissues conductive elements

[1] In the stem of *Cuscuta* and in parasites generally, the hadrome but not the leptome is less developed than in green plants of similar size. Occasionally, also, parasitism checks the growth of the organs infested by the parasite, the conductive tissues as well as the others having a reduced development.

play the most important part, many parenchymatic cells growing into tracheids and becoming of importance in conducting water and salts to the growing shoots. Similarly, when a leaf of *Torenia* is placed upright in the soil, it gives rise to a shoot; the dorsiventral petiole develops into a radially symmetrical organ, and new vascular bundles develop from parenchyma, forming a vascular cylinder comparable to that of the stem. In many similar instances, where there is an increased flow of substances through the parenchyma, some of the cells in the latter may become transformed into tracheids; for example, when vascular bundles are severed, tracheids and even tracheae may develop from parenchyma cells, in some cases forming connecting " bridges " of conductive tissue between the several bundles and neighboring intact bundles. When scale primordia grow into leaves in air and light, there is a much greater development of vascular tissue than when they grow into scales in soil or darkness. When seedlings are deprived of leaves, or when they have smaller leaves than usual, or are otherwise poorly nourished, the bundles are smaller than when the seedlings are well-nourished.

So far as known, changed conditions cause much less variation in leptome than in hadrome. However, an increase in sieve tubes has been observed in *Ipomoea* and *Raphanus* grown in solutions of saccharose or glucose; sometimes in such conditions sieve tubes appear even in the hadrome. Remarkable variations have been observed in roots subjected to lateral pressure; for example, in *Pisum* the primary root, commonly triarch, becomes tetrarch under pressure, and the side roots become polyarch; the commonly pentarch roots of *Vicia faba* similarly become hexarch. In the pine the number of bordered pits increases with the altitude.

The vascular tissues of lianas. — The relative area occupied by the vascular tract in lianas usually is greater than in other stems of similar proportions, and the individual elements possess unusual length and size; the Cucurbitaceae with their capacious vessels and sieve tubes furnish a familiar illustration. Many woody lianas exhibit peculiar secondary tissues; for example, *Bignonia capreolata* has radial plates of phloem penetrating far into the xylem, thus appearing like a cross in section (whence the name cross vine). In *Mucuna* there are alternating rings of phloem and xylem, and in *Rhus toxicodendron* a cross section of the climbing stem is strikingly eccentric, owing to the much greater wood development on the side toward the support. That the characteristic structural features of lianas may be due in part to external factors is clear from the fact that in *Vitis vinifera* the vascular tract in climbing stems is much more differentiated than in stems that do not climb. However, lianas have been inadequately studied, and little is known concerning the cause or significance of their peculiar secondary tissue.

Variations in secondary wood due to external factors. — *The annual ring.* — In most trees and shrubs of temperate climates growth is much

more vigorous in spring than later, the *spring wood* being characterized by large thin-walled vessels, and the summer or *autumn wood* by small thick-walled vessels (fig. 326). The contrast between the spring wood and the autumn wood often is the chief circumstance which makes it easy to discern the *growth rings* of trees. The theory has been advanced that the decreasing size of vessels from spring to autumn is due to the gradual increase of pressure to which the growing tissues underneath the bark are subjected. A more tenable theory, harmonizing better with conditions in primary conductive tissues, is that the size and number of the cells and the thickness of the walls are greatest in spring, because the ascent of sap is more active then than later. The new cells take part in this movement, and from the ascending materials derive the substances used in their development. Here, then, as in primary hadrome, maximum growth is correlated with a large movement of materials.

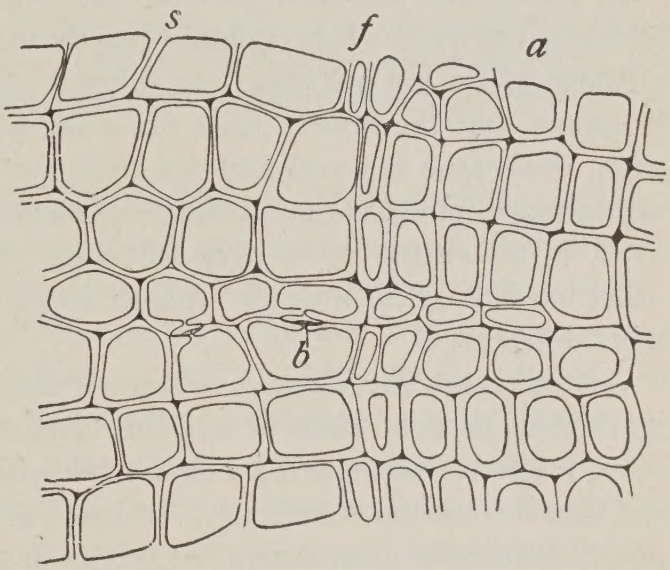


FIG. 326. — A cross section through an annual ring in the secondary wood of the Austrian pine (*Pinus laricio*), showing the large-calibered vessels of the spring wood (*s*) and the small-calibered vessels of the preceding autumn wood (*a*); note the relatively sharp line (*f*) between the autumn wood and spring wood; *b*, bordered pits in cross section; highly magnified.

Variations in the width of annual rings. — The width of the annual ring is subject to considerable variation, which is dependent in part upon the age of the tree and in part upon seasonal conditions. In early life there is a *period of acceleration*, during which the width of the rings usually increases from year to year, probably because of the increased absorption and food supply which are made possible by a more extensive root system and by a greater expanse of foliage. Even if the rings are of equal width year by year, there is an increasing increment of tissue, owing to the enlarging circumference. After some years, which may be few or many according to the species, there comes a *period of maturity*, characterized by approximate constancy in the

annual increment. Finally, there is a *period of retardation*, which is marked by an actual decrease in the amount of tissue laid down year by year, the annual increment approaching zero in extreme old age. While new roots and branches develop yearly throughout life, the loss of old branches by death finally exceeds the gain, and it is possible also that in an aging tree a given amount of leaf or root surface becomes less effective. In long-lived trees (such as the oak, chestnut, or yew) the final period may not begin for 150 or 200 years, and may continue some hundreds of years thereafter.

In young and middle-aged trees there often are such large fluctuations in the width of the annual rings that the progressive phenomena outlined above are not easily recognized. Careful observation makes it appear that the growth rings are wider and the cell caliber greater when the season is warm and dry than when it is cold and wet, thus appearing to indicate that strong transpiration facilitates the development of secondary as of primary wood. Stem elongation, on the other hand, is greatest in wet seasons, being facilitated by weak transpiration (p. 251).

Annual rings and climate. — Annual rings are much more sharply marked in periodic than in uniform climates, the greatest difference being found where there is a well-defined winter and summer, or where wet and dry seasons alternate. In uniform climates annual rings are poorly marked or even absent, especially in the most pronounced evergreens (such as the conifer, *Araucaria*). The trees of eastern Java, which has alternate wet and dry seasons, have much more prominent growth rings than those of the uniform climate of western Java; even species that are common throughout (as the teak, *Tectona grandis*) have uniform wood in the latter region and growth rings in the former. In the teak the difference produced directly by climate is accentuated by the fact that the tree is evergreen in western and deciduous in eastern Java. That the deciduous habit favors ring formation is shown generally by the presence of more prominent rings in deciduous than in evergreen trees in the same climate. Probably the sudden cessation and renewal of activity in deciduous trees as compared with the less interrupted growth of evergreen trees sufficiently account for their more pronounced ring development. The continued appearance of annual rings in certain European trees transferred to uniform tropical climates shows that hereditary as well as environmental factors may be of influence.

Where the climate is detrimental to tree growth, as in alpine and arctic regions, the annual rings frequently are eccentric rather than concentric, and are exceedingly narrow, sometimes being discernible only upon microscopic examination; a *Juniperus* stem has been reported as having a diameter of only thirty centimeters and yet exhibiting four hundred rings. Some of the large polar kelps have a tissue differentiation suggesting annual rings, there being alternating regions whose differences probably are due to seasonal variations.

Rings other than annual. — Sometimes two rings are developed in a single year, as when a prolonged summer drought is followed by a pronounced wet period, or when a tree puts forth new leaves after defoliation by insects or by storms, the new foliage being accompanied by a second cylinder of "spring wood." Some tropical trees shed their leaves two or three times a year, and in such cases the number of rings coincides with the number of times the leaves are shed; for example, a *Theobroma* tree known to be only seven-and-a-half years old had twenty-two rings. In *Dioon* and perhaps in other cycads, rings are not formed annually, but once in every ten or twenty years.

Concluding remarks on vascular variation. — Differences in the flow of materials through conductive tissues appear to be the chief cause for their structural differentiation, both in primary and in secondary wood. Nearly all cases of increased vascular development, whether involving an increase in the length, caliber, or number of the elements or in the thickness of the walls, can be referred to increased conduction; this may result either from high transpiration, as in desert regions and in other situations that are exposed to desiccation, or from an increased flow of structural materials, as in secondary wood and in plants attacked by parasites. In the weak development of wood in alpine and polar regions, unfavorable conditions for absorption seem to outweigh the otherwise favorable influence of strong transpiration. The conductive tissues appear to furnish the best evidence found in the plant kingdom in favor of the idea that organs increase through use; however, it is a more tenable assumption that an increased flow provides more adequately the materials requisite for enlargement and perhaps also the physical stimulus needed for continued growth.

The rôle of vascular tissues. — *The hadrome.* — The hadrome forms the pathway of ascending water, as is evident from the quick wilting of the leaves when a complete section of wood is removed, and from their continued turgescence when a cylinder of bark is removed. The ascent in tracheids and tracheae of water colored with eosin has been microscopically observed, and the cessation of such movement, when these tissues are infiltrated with cocoa butter, gelatin, or paraffin, has been demonstrated. In the hadrome also there ascend inorganic salts in

solution in the water. While it is generally believed that the movement of water is through the lumina, some observers have held that the lignified walls are the chief paths of conduction. There is no adequate disproof of wall conduction; the stoppage of movement by paraffin infiltration is often cited as such, but it is probable that the walls as well as the lumina are infiltrated. If, as is now generally believed, the ascending water forms a continuous column involving the entire hadrome, the walls would appear to play an important part in conduction, though doubtless subordinate to the lumina.

Structural advantages of tracheae and tracheids. — The great elongation of the hadrome elements probably facilitates conduction, movement through elongated lumina being supposed to be more rapid than through a series of short lumina separated by walls. Tracheae thus may be better conductive elements than tracheids, though the latter certainly are efficient, since they alone are present in the conifers, which include the tallest known trees. In some conifers, as the larch, conduction has been shown to be essentially as rapid as in dicotyls. Perhaps the conductive efficiency of conifer wood is due in part to its relatively long tracheids. Doubtless the large caliber of the hadrome elements also facilitates conduction. The large and long hadrome elements of lianas may be regarded as very advantageous, since the length of the stems is so great in proportion to their diameter. Oblique end walls have been thought to be more advantageous than horizontal end walls because they present a greater diffusion surface.

The advantages of differential lignification. — Lignification is highly beneficial, since *lignin*, which is the chief factor in giving rigidity and strength to woody tissues, is at the same time permeable to water and solutes. The slightly lignified spiral and annular vessels are not so strong and rigid as are the larger and more lignified pitted, reticulated, and scalariform vessels, which may be regarded as the main conductive elements. Though the entire wall is permeable, the thin spots or pits probably represent more permeable regions which facilitate rapid lateral transfer, without interfering with the mechanical efficiency of the wall. Bordered pits are supposed to act somewhat in the manner of a valve, opening when the pressure on the two sides is equal and closing when it is unequal, a pressure difference of one fifteenth of an atmosphere being sufficient to cause closure; thus bordered pits may either facilitate or impede lateral transfer.

The advantages of dead tissues in conduction. — One of the chief advantages of tracheids and tracheae is associated with their early death. Water and solutes pass through living cells by osmosis, their rate and direction of movement being independent of one another; the

movement of any given solute is conditioned by the permeability of the cell walls and the protoplasmic membranes for that particular solute, and by differences in its pressure in adjoining cells. In the dead hadrome, however, water and solutes may move together for great distances without passing protoplasmic membranes and only occasionally traversing cell walls, movement being much more rapid than by diffusion through living cells. Except for a few cells in the epidermis and cortex of the root and in the mesophyll of the leaf, the entire course of water through a plant is in dead tissues. The streaming of protoplasm, a phenomenon especially common in water plants, sometimes may facilitate conduction in living cells.

The rôle of sieve tubes. — The sieve tubes generally are regarded as organs of protein conduction, partly because they are living elements rich in protein, partly because they form a continuous system of tubes comparable to the water-conducting elements, partly because the porous sieve plates seem well fitted for the passage of viscous albuminous materials, and partly because no other tissues are known that are peculiarly fitted for protein conduction. The girdling of trees often results in increased growth above the girdled area, and under favorable conditions roots originate from that region. Such phenomena appear to indicate that there is in the bark a downward movement of foods and that they tend to accumulate above the girdled portion, furnishing the materials used in the extra growth. Trees often are killed by complete girdling, probably because of the inability of the food to reach the roots. In those dicotyls which have sieve tubes inside the hadrome none of the above-noted effects of girdling are seen.

Sieve tubes have been variously regarded as organs of protein accumulation, as organs of protein manufacture, and as structures that are well fitted for the propagation of stimuli. The conduction theory, however, seems most tenable, though the actual movement of material has not been well observed. Movement is from regions of high to regions of low pressure and may be downward toward the roots, outward toward the branches, or upward toward the flowers and fruits. Owing to the chemical similarity between the protoplasm and the conducted protein, it may be regarded as advantageous or even necessary that the conducting cells be living. The closing of the sieve plate in winter by a callus may be advantageous, but more probably it is of no particular significance. Nothing is known concerning the rôle of the companion cells, which in angiosperms persistently accompany the sieve tubes and even extend beyond them in the bundle termini.

Conduction in the lower plants. — The sieve tubes of the larger algae commonly are supposed to be organs of protein conduction, but this has not been proved. The rise of colored fluids has been observed in the " vascular " tract of moss stems;

it is not known that movement is more rapid there than in the other stem tissues, though the greater cell elongation makes it seem probable.

The path of carbohydrate conduction. — Sugar passes readily from cell to cell by osmosis, and it is probable that the cortical parenchyma is the chief tissue involved in its conduction, though carbohydrate as well as protein may pass along the sieve tubes; the ill effects of girdling may be due as much or more to the cutting off from the roots of carbohydrates as to the cutting off of proteins. The endodermis, because of its rich starch content, has been regarded as a region of carbohydrate conduction, but it is much more probable that it is a layer in which surplus starch accumulates. Much of the carbohydrate that descends in the cortex and leptome during the summer and autumn may ascend in the wood with water and soil salts the following spring, as in the sugar maple, whose sap may contain as much as three per cent of sugar.

Advantages associated with various bundle arrangements. — The grouping of conductive elements into strands is advantageous, partly because of the consequent economy in space and structural material in the protective stereome as well as in the hadrome and leptome, but more particularly because continuity thus is made possible. In the bundle the hadrome seems to have the place of advantage. In the stem it is inside the leptome, where there is greater freedom from mechanical strains, and where dangers incident to transpiration are more remote. In the leaf (even in ferns, where the stem bundles are concentric) the hadrome is uppermost, and therefore closest to the most active food-making region. Even in roots the hadrome occupies equally with the leptome the place of advantage, that is, nearest the cortex, from which food materials come and to which organized foods go.

There has been advanced the very dubious hypothesis that a " struggle for existence " has taken place between the tissues, and that the stronger element, the hadrome, has " won " the place of advantage. In secondary tissues it is highly advantageous for the xylem, which gives rise to the permanent tissue, to be innermost, since the less permanent tissue may then exfoliate as the other develops. Where other conditions obtain, as in some lianas (*e.g. Mucuna*) and in monocotyls (as *Cocos*), temporary and permanent tissues are intercalated in such a way as to make impossible the development of a solid cylinder of permanent tissue; in *Cocos* the decay of the temporary elements leaves the wood in disconnected strands, whence the name, porcupine wood.

The slight reduction of leptome in hydrophytes is advantageous, for while submergence results in reduced water conduction, protein conduction is as prominent as ever. The large development of leptome in lianas having bicollateral bundles may facilitate protein conduction in the long slender stems just as the elongated and

enlarged hadrome elements facilitate water conduction. The great development of hadrome in xerophytes appears disadvantageous rather than advantageous.

In secondary wood, conduction is mainly in the alburnum, where living parenchymatous cells are intercalated among the dead vessels, the medullary rays furnishing lateral connections between the alburnum, cambium, and phloem. The dead duramen often is a region of accumulation of waste products (p. 240), the vessels being filled with tannins, gums, and other excreta. Sometimes vessels are closed by *tyloses* which arise through the intrusive growth of neighboring parenchyma cells. Tylosis formation characterizes especially the transformation of alburnum to duramen, representing the final phase of activity in the wood parenchyma. Tyloses develop also at wounded surfaces and in the vascular tracts of certain plants attacked by parasites; in these cases they clearly are advantageous in checking conduction, but no particular advantage or disadvantage is apparent in the clogging of duramen tissues.

The rôle of the pericycle and of the endodermis. — The chief rôle of the pericycle, which is a meristematic layer, is the origination of new lateral organs, especially roots. The endodermis often is a protective layer, particularly in roots and rhizomes, its suberized walls serving to check local losses of water from the bundle. In aerial stems it may serve as a region of starch accumulation, whence the name starch sheath.

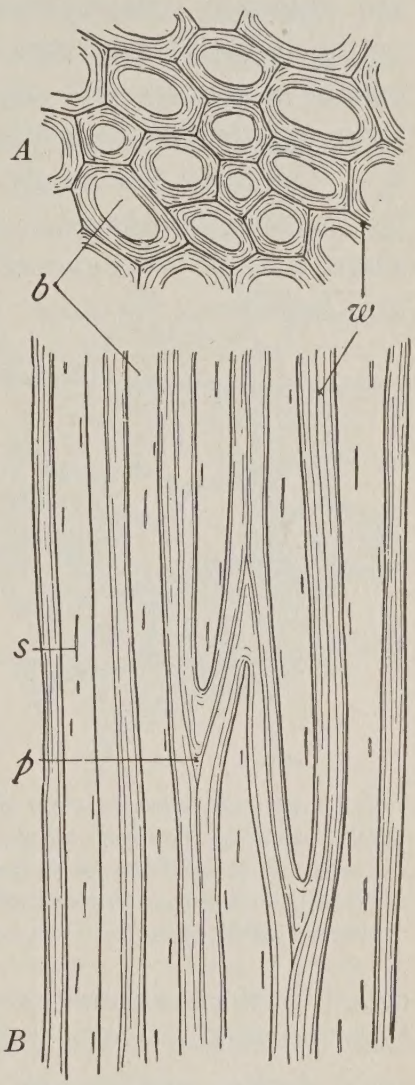


FIG. 327. — Bast fibers of the century plant (*Agave americana*): *A*, a cross section through a bundle of bast fibers, showing the uniform stratification of the walls (*w*), and the small size of the lumina (*b*) in proportion to their thickness; *B*, a longitudinal section through such a bundle, showing prosenchymatous cell ends (*p*) dove-tailing with one another; *s*, spirally arranged wall slits; other lettering as in *A*; highly magnified.

4. MECHANICAL TISSUES

Introductory remarks. — In small land plants and in water plants of all sizes mechanical tissues are poorly if at all developed, their rigidity when present being due to the cell walls and to turgor. Large aerial and soil organs, however, are subjected to considerable strain, and conspicuous mechanical tissues commonly are present, insuring the maintenance of form and position.

The mechanical elements or stereids. — *Bast and wood fibers.* — The most representative mechanical elements are the *bast fibers*, which are especially characteristic of the phloem. They are elongated prosenchymatic structures with attenuated points, and thus have long regions of contact with adjoining fibers in the same longitudinal row, insuring a degree of dovetailing perhaps unequaled elsewhere (fig. 327, B). The fibers commonly average one or two millimeters in length, but in ramie (*Boehmeria*), one of the most important fiber plants, the length may be two hundred millimeters or more. Bast fibers are multinucleate from the outset (*i.e.* they are *coenocytes*) and they remain alive much longer than do tracheids or tracheae. The walls are highly thickened with cellulose or occasionally with lignin, the material being deposited in regular centripetal layers; the stratification incident to differential or periodic deposition often is very evident (fig. 327, A). In the mature fiber the lumen is extremely small, the volume of the wall being many times greater. The walls are marked by spirally arranged slits, suggesting that the ultra-microscopic particles (*micellae*) also are spirally arranged like the strands of a rope. *Wood fibers* (also called libriform elements) resemble bast fibers, differing therefrom in their restriction to secondary wood, and in their lignified walls and early death; furthermore, they are not coenocytes. There are all gradations between wood fibers and tracheae, whereas bast fibers are contrasted rather sharply with other phloem elements.

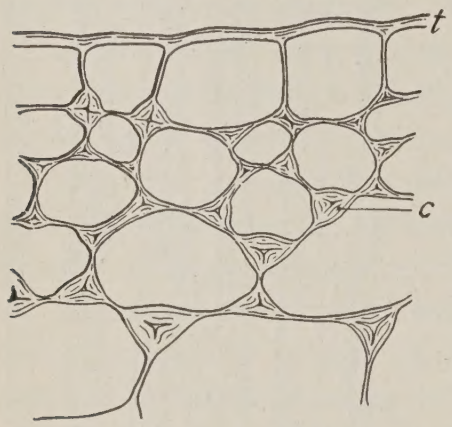


FIG. 328. — A cross section of a *Begonia* petiole, showing collenchymatic thickening (*c*) of the walls at the angles of the outermost cortical cells; *t*, cuticle; highly magnified.

Collenchyma. — *Collenchyma* is a term applied to living mechanical tissues made up of elongated cells whose walls are unequally thickened with cellulose of high water content (sixty to seventy per cent, as against twenty to forty per cent in bast), the thickening often being most pronounced at the cell angles (fig. 328). Unlike bast, collenchyma is capable of growth elongation, and the walls are much more refrangible. In addition to the permanent collenchyma, which is characteristic of the cortical region of stems and petioles, temporary collenchymatic thickening often occurs in bast primordia.

Sclerenchyma. — Representative *sclerenchyma* cells or *sclereids* are mechanical cells that cannot be classified as collenchyma or as bast, though bastlike fibers in the cortex often are called sclerenchyma. The most characteristic sclereids are the hard, stiff, and relatively isodiametric *stone cells* with brownish lignified walls, which are found in the secondary bark of trees and in the shell of the hickory nut, and which arise through the *sclerosis* of ordinary parenchyma cells (fig. 329). Sclereids of this sort have stratified walls due to differential centripetal growth, the walls being traversed by more or less branched canals, along which the structural materials probably have passed. The cells die soon after stratification ceases.

The stellate mechanical cells of water lily leaves (fig. 109) and the T-shaped prop cells of *Osmanthus* (fig. 244) may be classed with sclereids. The rigidity of stems is not due entirely to bast, collenchyma, and sclerenchyma, other tissues with thickened walls, such as the wood and the cutinized epidermis, playing an important part. In *Equisetum* and in various grasses (notably the cereals), considerable silica is deposited in the walls, giving them considerable rigidity.

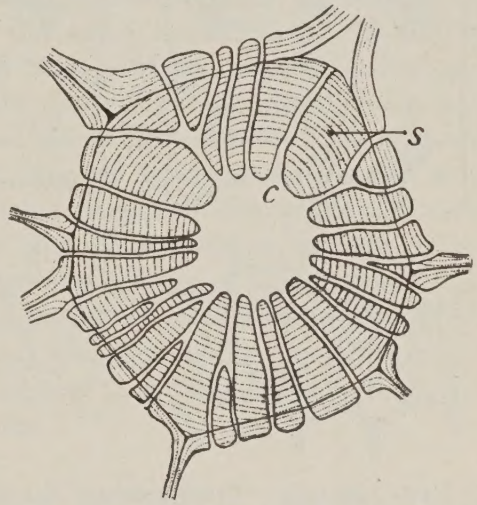
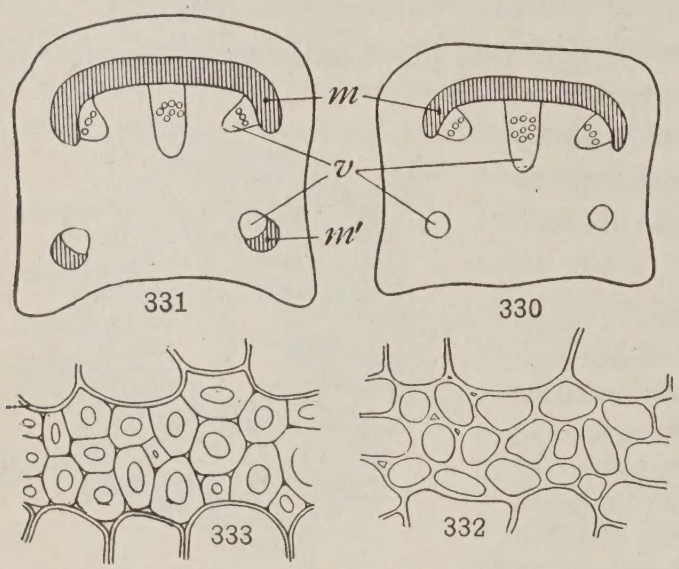


FIG. 329. — A stone cell or sclereid from the petiole of the wax plant (*Hoya carnosa*); note the lines of stratification (*s*), representing successive periods of wall construction, and also the canals (*c*) which connect the lumina of adjoining cells, and which have remained open during wall-building; highly magnified.

The distribution of stereome in plants. — Many sclereids occur as idioblasts, being scattered irregularly through various tissues, as in the bark of trees. More commonly the mechanical elements are grouped in strands, the most usual condition being the association of mechanical and conductive elements into a fibrovascular bundle. As a rule, compact strands of bast fibers occur just outside the leptome (fig. 61), and sometimes there is a mechanical cylinder entirely surrounding the vascular bundle (fig. 335), or even the whole vascular region (fig. 334). In monocotyls (especially in xerophytic species) there usually is a progressive decrease of bast strands inward, the outer bundles having conspicuous mechanical strands outside the leptome, while often the inner bundles are without them. In many xerophytic leaves and stems there often are cortical strands of bastlike fibers, especially just beneath the epidermis; similar

strands are frequent also in the bark. Wood fibers rarely are grouped in compact strands, but individual fibers with all intergrading stages are scattered here and there among the conducting elements.

The influence of external factors upon mechanical tissues. — *Mechanical stimuli.* — An unattached tendril has less tensile strength than one that is attached, the latter sometimes being two to five times stronger than the former. Frequently this change in tensile strength is associated with a structural change, more mechanical cells being developed or further wall thickening appearing in those already present (figs. 330–333). In some cases collenchyma develops into bast upon the attachment of the tendril. It has been claimed that growing stems of *Helleborus* subjected to tension develop bast in regions where ordinarily none is present; furthermore, stems subjected to tension for three days have been found able to support a weight of 3500 grams, while at the inception of the experiment only 400 grams could be supported. These striking results, though frequently tested, have not been confirmed, either in *Helleborus* or in other plants, though it appears that certain stems when exposed to tension for some days or weeks become somewhat stronger; furthermore, the bast fibers and hadrome elements become somewhat more numerous and have slightly thicker walls than in controls not so exposed. In many cases tension appears to cause no appreciable change.



FIGS. 330–333. — Cross sections of tendrils of *Cyclanthera explodens:* 330, a diagrammatic cross section of a tendril that has not come in contact with a support; 331, a diagrammatic cross section of a tendril that has come in contact with a support; note the larger size of the tendril, the increased development of the chief mechanical strand (*m*), and the development of accessory mechanical strands (*m'*); *v*, vascular tracts; 332, a portion of the mechanical strand of 330, highly magnified, showing collenchymatic wall thickening; 333, a portion of the chief mechanical strand of 331, similarly magnified; note the highly thickened walls, the elements being bast rather than collenchyma. — From HABERLANDT.

In pendent fruits (as the apple) the tension on the fruit stalk increases constantly as the fruit gains in weight, also the strength of the stalk increases from week to week, although it has been shown that the increasing pull of the fruit is not a determining factor of importance. The fruitstalks of *Cucurbita*, however, have more mechanical tissue when the fruits hang free in the air than when they rest on the ground. It is claimed by some investigators that compression is more effective than tension in stimulating the growth of mechanical tissue. Roots react to mechanical stimuli more readily than do stems, tension resulting in a conspicuous increase in the number of mechanical elements and in the thickness of the walls, and compression resulting in a decreased cell size and in an increased wall thickness.

If a young tree is fastened so that it can sway in but one plane, its diameter in this plane will be greater than in any other. Probably the elliptical cross section seen in trunks of seacoast trees is caused by wind, the long diameter being perpendicular to the coast line. In the spruce the upper side of a horizontal branch is composed largely of white wood and the lower side of red wood, the former having about twice the tensile strength of the latter; the red wood, whose elements have thicker walls, possesses the greater compression strength. The upper part of a branch is subjected to tension and the lower part to compression, and the differences observed may thus be explained; gravity also is believed to be an important causative factor. Red wood occurs also on the lee side of branches exposed to wind. In dicotylous trees the differences of wood are less marked than in conifers, and mechanical tissues are, if anything, better developed on the upper than on the under side of horizontal branches.

Desiccation. — While the influence of mechanical stimuli is not clearly understood, desiccation is known to favor the increased development of mechanical tissue. In dry air a mechanical cylinder is developed in the stem cortex of *Mentha aquatica*, while in moist air the cells remain parenchymatous. In the stem of *Ficus scandens* the cells that become collenchyma in moist air become bast in dry air. In deserts plants of irrigated soil show less mechanical tissue than do those of dry soil. Aquatic and terrestrial stems of the same species (as *Polygonum amphibium*, figs. 127, 128) differ widely in the amount of mechanical tissue developed, the water form being too weak to stand alone, whereas the air form is very stiff and rigid. Fern roots in moist soil have a slight development of mechanical tissue, the cells being few and the walls thin. Probably it is generally true that bast, collenchyma, and sclerenchyma cells increase in number and in wall thickening as the tissues in which they are developing are exposed increasingly to desiccation. The minimum of mechanical tissue occurs where transpiration is reduced to zero, namely, in the water. Observation confirms experiment, for mechanical tissues are less developed in hydrophytic than in other habitats (figs. 94, 325), reaching their culmination in xerophytes.

The rôle of mechanical tissues. — *The mechanical features of stereids.* — The fact that ropes and cables are made from the bast fibers of hemp, ramie, etc., indicates the tensile strength of bast strands. While the strength of ordinary parenchyma, as pith, is but one kilogram per square millimeter, some of the strongest bast has within its limits of elasticity a tensile strength of twelve to twenty-five kilograms per square millimeter, the higher figure being twice that of wrought iron and about equal to that of German steel; however, the breaking point of steel is much beyond that of bast. Bast differs widely from the metals in having a considerable degree of elastic elongation, and is itself exceeded in this respect by the mechanical strands of lichens, those of *Usnea* being capable of elongating sixty to one hundred per cent (see fig. 419). Bast is considerably stronger when desiccated than when it contains moisture, though it is more elastic in the latter condition; lignification usually decreases the tensile strength. The great tensile strength of bast is due to the amount and quality of the wall thickening, to the dovetailing of the prosenchymatic cells, and probably, also, to a spiral arrangement of the wall micellae. The fact that the limit of elasticity is so near the breaking point is not disadvantageous, since any elongation of bast beyond the limit of elasticity would be harmful. Collenchyma is almost as strong as bast, though it has a lower limit of elastic elongation. Having the power of growth elongation, it is especially suited to growing tissues.

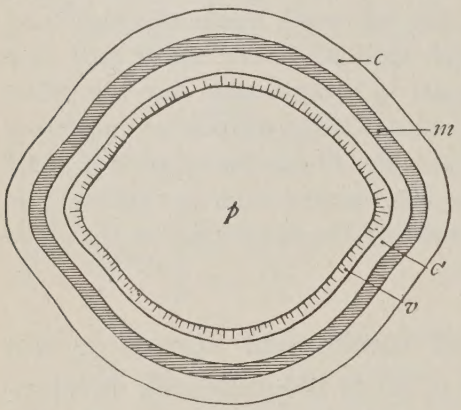


FIG. 334. — A diagrammatic cross section of a carnation stem (*Dianthus caryophyllus*), showing the development of a mechanical cylinder (*m*) outside the vascular tract (*v*); *c*, *c'*, cortical parenchyma; *p*, central pith.

The rôle of scattered sclereids is less obvious and probably less important than is that of bast and collenchyma though it is of significance in certain leaves (p. 153). Bast and collenchyma sometimes have been regarded as advantageous in checking transpiration, and collenchyma sometimes is considered to be a sort of "water storage" tissue. The latter theory may be dismissed summarily, and the former theory is at least doubtful, in view of the permeability of the walls.

Flexile strength. — The flexion of a stem induces tension on one side and compression on the other, each strain decreasing to zero at the center. Consequently a stem with a strong cylinder of peripheral

mechanical tissue may have a central region of pith or may even be hollow (as in *Equisetum* and in the grasses) and yet have considerable rigidity. It has been computed that if the mechanical periphery forms one seventh of the diameter, the strength will be sufficient to meet all usual strains. Further development of mechanical tissue would be not only useless but actually disadvantageous, because it would require a considerable amount of structural energy and material, and also because space would be used that might be taken by other tissues. The average erect herbaceous stem illustrates admirably these mechanical principles. Sometimes (as in *Dianthus*, fig. 334) there is a mechanical cylinder surrounding the leptome, while in other cases strands of bast form an interrupted cylinder. External to the bast is the collenchyma cylinder, and internal to the bast is the cylinder of secondary wood which is of great mechanical importance. Although the conductive and mechanical bundles in monocotyl stems are scattered, the decrease of bast elements toward the center results essentially in a broken peripheral cylinder of mechanical tissue (fig. 335). In angled stems (notably in the mints, fig. 336) strains are accentuated at the angles, where there is considerable collenchyma just inside the epidermis, and often a bast crescent just outside the leptome.

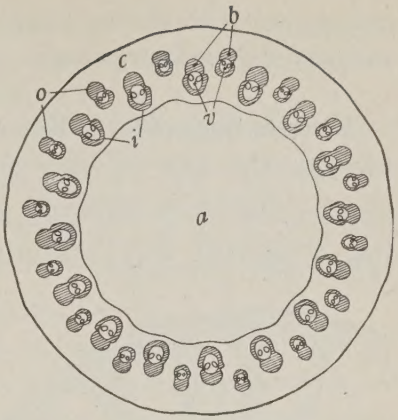


FIG. 335. — A diagrammatic cross section of the erect aerial stem of *Juncus balticus littoralis*, showing an interrupted mechanical cylinder, composed of alternating outer (*o*) and inner (*i*) fibrovascular bundles, in which a bast cylinder (*b*) surrounds the vascular tract (*v*); note that the bast is more strongly developed outward than inward; *c*, cortex; *a*, large central chamber, originally occupied by pith cells; considerably magnified.

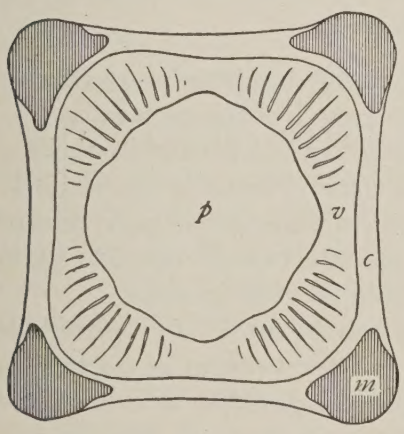


FIG. 336. — A diagrammatic cross section of an erect aerial stem of a mountain mint (*Pycnanthemum virginianum*), showing columns of mechanical tissue (*m*) at the stem angles; *c*, cortical parenchyma; *v*, vascular cylinder; *p*, central pith region.

The advantage of flexile strength is well illustrated on mountain slopes that are subject to snowslides and avalanches, flexible trees and shrubs (such as alders and willows) being uninjured, whereas some rigid trees (as conifers) snap off like pipe-stems. In lowlands the ac-

cumulation of ice during a cold rain frequently causes the rupture of branches that withstand all ordinary strains.

Tensile strength. — Resistance to tension depends not on the position but on the size of the mechanical strand. However, since tension almost always is unequal, hence involving flexion, a massing of strands into a central, solid cylinder is most advantageous, since the danger of rupture through differential strain is reduced to a minimum. Roots are subject to considerable tension, especially when the stems sway in the wind, and they differ from erect stems somewhat generally in that the central portion is occupied by thick-walled wood cells of considerable strength instead of by a core of pith. Rhizomes (as in *Lathyrus* and *Juncus*, fig. 337) are subject to the same tensions as are roots, and like them differ from erect stems in the absence or weak development of central pith. The relatively central vascular tract usually has thick-walled wood elements, and there may be a mechanical cylinder or scattered mechanical strands outside the wood.

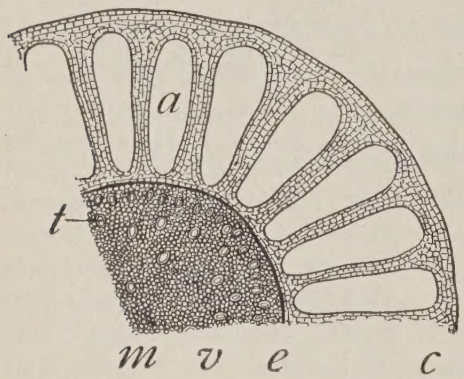


FIG. 337. — A diagrammatic cross section of the rhizome of *Juncus balticus littoralis;* note the symmetrically arranged air chambers (*a*) in the cortex (*c*); *e*, endodermis; *v*, vascular tract, composed of a matrix of mechanical cells (*m*) surrounding groups of conductive vessels (*t*).

Lianas are subject to rather extraordinary strains, the combination of tension, flexion, and pressure in a woody twiner, owing to the growth of the supporting tree, being especially severe; in such stems there is a large development of bast and of thick-walled wood. In tendril climbers much of the strain is borne by the relatively slender tendrils, which often have central mechanical tissues that may become strengthened on attachment. In flattened and spirally twisted tendrils (as in *Echinocystis*) the strains are similar to those sustained by twining stems.

Submersed stems, especially in running streams, may be subject to considerable tension, but the conditions are such as to oppose the development of mechanical tissue; however, the vascular tract usually is in a central position, as in roots and rhizomes, and therefore situated where the strain is least (fig. 94). The absence of rigid mechanical tissues is distinctly beneficial in such plants as *Nereocystis* and the water lilies, since the floating synthetic organs thus are enabled to rise and fall with the water. Furthermore, the absence of mechanical tissues and the consequent easy rupture of the stems favor vegetative propagation.

Pendulous organs, such as fruit stalks, commonly have central mechanical strands. Thus the most diverse of organs, namely roots, rhizomes, tendrils, sub-

mersed stems, and pendulous stalks, organs which agree only in frequent or constant exposure to tension, have central mechanical tissues, contrasting with the peripheral mechanical tissues of erect herbaceous stems.

Compression strength. — The trunks of trees are subject to compression, owing to the weight of the parts above. Longitudinal pressure of this sort requires columnar strength. In many trees (as in the walnut, red cedar, and most conifers) there is a solid supporting column whose central portions are the hardest and strongest, but in some instances (as in the sycamore) the supporting column may become a hollow cylinder, owing to the decay of the heartwood.

Roots and rhizomes are subject to radial pressure as they grow in diameter. A peripheral mechanical cylinder is the most effective means of resisting such radial pressure, and this is present in many rhizomes in addition to a central mechanical strand. Prop roots (fig. 40) are subject to unusual strains, since stem flexion causes severe tension on one side of the plant and equally severe compression on the other. The prop roots of corn often contain both central strands and peripheral cylinders of mechanical tissue, so that they are well fitted to withstand strains of every sort.

5. THE PROTECTIVE RELATIONS OF STEMS

Introductory remarks. — The greatest of dangers to plants is excessive transpiration, and to this the aerial stem is especially exposed; indeed, in deciduous trees and shrubs the aerial stem is the most exposed of all organs, since it alone is subject to transpiration and to other aerial dangers during periods of drought or cold. Aerial stems are structurally the best protected of plant organs, save only seeds. In many cases the stems, as well as the leaves, are deciduous, and in such plants protective structures usually are much less developed, their habit of life constituting their chief protection.

Epidermis. — In aerial herbaceous stems the protective tissues resemble those of leaves (p. 83), the outer epidermal walls being highly cutinized, while waxy coats and hairy coverings occur in many cases. In the European mistletoe (*Viscum album*) and in one of the maples (*Acer striatum*), the epidermis, through continual radial division, remains as a relatively permanent layer, a forty-year-old trunk of the latter sometimes being covered with a true epidermis.

Bark. — In most trees and shrubs the inception of secondary growth is followed by the rupture and exfoliation of the epidermis and of portions of the cortex. Thenceforth the protective tissues generally are called *bark*, a term including the heterogeneous complex of living and dead cells outside the cambium ring. Apart from remnants of the epidermis and the primary cortex, the bark consists chiefly of the phellogen and its products and of the secondary phloem, the latter

including new living cells near the *cambium* (sieve tubes, companion cells, parenchyma), dead cells of similar character farther out, and mechanical elements (largely bast fibers). The development of the cork cylinder usually occasions the death of all cells external to it, since it checks the movement of material from within.

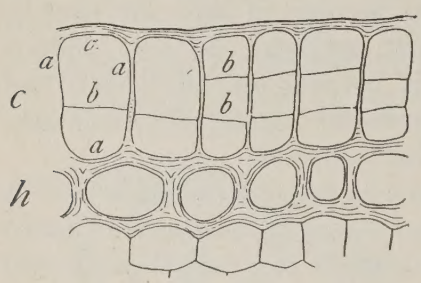
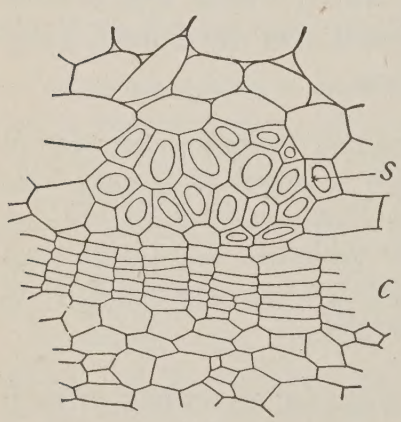


FIG. 338. — A cross section of the outer part of a stem of the boneset (*Eupatorium perfoliatum*), showing the development of epidermal cork (*c*); *a*, the original epidermal walls; *b* later cross walls, whose appearance indicates the inception of cork formation; note the thick-walled hypodermis (*h*) which forms a mechanical cylinder around the cortical parenchyma; highly magnified.

Cork. — *Structural features.* — The most important protective tissue of the bark is the *cork*, which is developed from a meristematic layer known as the *phellogen* or *cork cambium*. Occasionally this layer arises from the epidermis, as in some Rosaceae and in many herbs (fig. 338), but much more commonly the phellogen layer arises in the primary cortex (figs. 339, 340), as in most woody stems and in various underground stems (*e.g.* potato tubers). The region usually involved is the outermost cortical layer, the hypodermis, but phellogen may develop in any of the deeper layers, not excluding the endodermis; even the pericycle sometimes gives rise to



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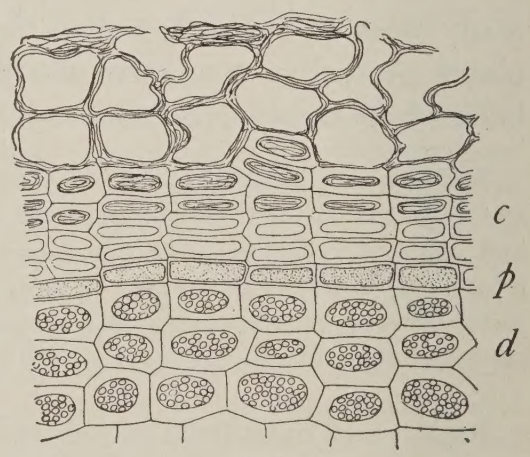

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FIGS. 339, 340. — 339, a partial cross section of a stem of *Jussiaea peruviana* from a dry habitat, showing the development of cork tissue (*c*) underneath a stereome bundle of thick-walled cells (*s*); from SCHENCK; 340, a cross section of the outer part of a bur oak twig (*Quercus macrocarpa*), showing the layers of the periderm; *p*, the phellogen, from which cork (*c*) develops externally and phelloderm (*d*) internally; note that the phelloderm contains chloroplasts, that the cork layer is without air spaces, and that the tissues external to the cork are rupturing; both figures highly magnified.

cork. Cork is developed outward from the phellogen layer, which toward the inside may give rise to *phelloderm* or *cork cortex;* the phellogen, cork, and phelloderm together are known as *periderm.* Eventually this phellogen layer ceases its activity and a new phellogen layer develops underneath the old, though in some cases the original periderm layer persists for years (as in the silver fir), or even throughout life (as in the beech), the lateral growth of the phellogen keeping pace with the annual increase of the secondary wood.

The phellogen consists of delicate plasmatic tabular cells, which divide tangentially, the outer half becoming cork, while the inner remains phellogen and divides again. The cork cells also are tabular, and, as there is little displacement or radial division, they are arranged in radial rows. The walls soon become partly or wholly suberized, that is, a complex, fatty substance known as *suberin* replaces or is added to the original cellulose, after which the cells die. The walls of mature cork cells are brownish, the lumina containing air, and sometimes tannins, crystals, and other excretions; intercellular air spaces are practically wanting.

In the cork oak, which supplies commercial cork, the periderm layers are very thick. In certain trees (as in the winged elm, sweet gum, and hackberry) cork develops irregularly, forming peculiar warts, wings, or thorns. Often there are annual growth rings in cork tissues comparable to those in wood, broad layers of large cells alternating with thin layers of narrow cells. In the paper birch and in various other trees and shrubs, the bark is exfoliated in thin sheets or strips by reason of an alternation of dense and loose layers of this sort (fig. 341).

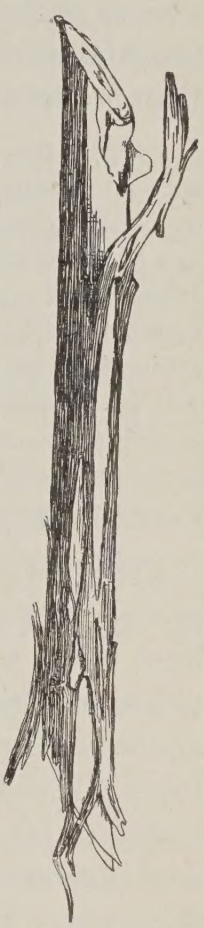


FIG. 341. — A portion of a stem of the nine-bark (*Physocarpus opulifolius*), showing the shredding of the bark into several thin exfoliating layers.

The influence of external factors upon cork development. — It has been shown elsewhere that under water, phellogen develops into aerenchyma rather than into cork, and that the development of cork layers beneath lenticels is favored by desiccation. Probably cork formation is favored generally by desiccation resulting from transpiration, the cells originating from the phellogen tending to deposit suberin, just as epidermal cells deposit cutin or surface wax under similar conditions. This view

is supported by the fact that on the inner side, where less exposed to desiccation, phellogen cells develop into phelloderm, which is a loose tissue resembling the complementary tissue of lenticels and the products of phellogen when developed under water. In the sassafras and probably in trees generally, cork formation is stronger on the lighted than on the shaded side of the branches.

Possibly the strong radial growth in developing phellogen is due to the fact that the path of least resistance is in the radial direction. When a branch is cut, the living cells bordering the wound are incited to active growth, and the wound is covered by a so-called *callus*, one of the most prominent elements of which is cork; such cork, arising from a phellogen layer originating in the callus, is known as *wound cork*. Probably the incitation to cambial activity is given by the increased flow of material arising from greatly accelerated transpiration, which also favors cork development. The direction of growth of the callus tissues is in the path of least resistance, that is, toward the exterior. When the cork layer of a potato tuber is exposed to strong radial pressure during its development, the chief cell divisions are radial, resulting in strong lateral growth instead of the usual radial growth.

The thickness of bark varies considerably with the habitat, being greatest in deserts and other dry situations and in alpine regions, and least in the tropical rain forest. Individuals of a species common to two situations have the thicker bark in the more xerophytic habitat; alpine and light cultures show more bark than lowland and shade cultures. Probably in most cases thick bark is associated with high transpiration and thin bark with low transpiration. The slight development of bark in roots and in rhizomes also is in harmony with this view. Thick bark in submersed stems does not invalidate this view, since increased thickness in such cases is due to the large development of air spaces (as in *Decodon*, pp. 68, 69).

The rôle of cork. — The conduction of food is the chief rôle of living bark, but the dead bark has a protective rôle of great importance because of the slowness of its exfoliation. The thickness of the bark with its large number of dead air-containing cells contributes to its protective efficiency, but the cork layer is by far the most significant feature. Partly because of the absence of air spaces, but more because of suberization, cork is about the most impermeable of tissues, and thus is of great value in checking transpiration. A potato that loses but 0.04 grams in weight in twenty-four hours if unpeeled, loses 2.56 grams if peeled, or sixty-four times as much, and yet the cork layer of a potato is so thin as to appear to the naked eye as a mere film. Twigs with the thinnest of cork layers transpire with almost inappreciable slowness,

if the lenticels and cracks are artificially sealed. Probably the chief value of cork is in checking transpiration in periods of relative inactivity, as in seasons of periodic drought or of winter cold, when there is little or no absorption; during such periods the exposed parts of deciduous trees and shrubs are completely mantled by an almost impervious coat of cork and bud scales.

Cork is relatively impermeable to air as well as to water, and after its formation, carbohydrate synthesis and aeration in subjacent tissues become greatly reduced, except in the neighborhood of lenticels. Cork is also a poor conductor of heat, so that changes of temperature are slower within the plant than outside. Cork prevents the invasion of living tissues by parasitic fungi and bacteria; a freshly cut surface of a potato tuber develops wound cork so rapidly that after twelve hours bacterial infection is impossible. Cork cells, like tracheids, tracheae, and bast fibers, are more efficient dead than living. Such local growths of cork as the wings of the winged elm and the warty projection of the hackberry are probably of no advantage to the trees producing them. Sometimes at the close of the vegetative season, bark is not perfectly " ripened," that is, it contains considerable water, and the various protective and mechanical elements are not fully formed. In many plants transferred from warmer to colder climates the shoots die back in the winter, because the vegetative season is too short to permit the ripening of the bark and wood.

Various bark features. — *Color.* — Young bark commonly is green, because the cortical chlorophyll is evident through the transparent epidermis. Soon the stem ceases to appear green, the chief cause of change in color being the development of the cork layer, whose opacity makes the chlorophyll invisible. The common bark colors are gray, brown, and black, but red occurs, as in some dogwoods, and white, as in some birches. As the tree matures, the characteristic bark color may be seen only on the younger branches, if the older limbs are furrowed. In a few cases, as in the mistletoe, moonseed, sassafras, and greenbrier, the relative freedom from cork formation permits the green color to remain evident longer than usual. Such green-stemmed trees as the bamboo and the banana are in reality gigantic herbs, in which ordinary bark does not develop. Often the exterior and the interior of the bark are differently colored, as in the hemlock, where it is black without and red within, and as in the yellow-barked oak, which is named from its inner bark, the outer bark giving rise similarly to the name, black oak. Bark colors, especially interior colors, often are due to the presence of various excreted products, such as tannins. Advantages in the various colors are not to be looked for.

Smoothness and roughness; exfoliation. — While the epidermis persists, young stems are smooth, except in the neighborhood of lenticels and *leaf scars;* the latter are of various shapes and sizes, and differ widely in the number and arrangement of the vascular strands, whose severed and healed surfaces are conspicuous as slight emergences within the scar (fig. 366). For a few years most stems remain smooth or smoothish, owing to the development of bark tissues as the stem increases in diameter. In some trees (as in the beech) continued lateral growth causes the bark to remain thin and smooth throughout life; the tropical rain forest in particu-

lar is rich in smooth-barked trees. In various palms the bark is soft and spongy, hence affording an excellent habitat for epiphytes. In most trees new phellogen areas develop at deeper levels or lateral growth fails to keep pace with diametral increase, so that the bark splits and becomes variously roughened. Some trees, as the bur oak, become furrowed very early, while others, as the basswood, remain smooth-barked for a long time, but ultimately become furrowed. "Alligator" bark is caused by the division of the bark into blocks by somewhat equidistant transverse and longitudinal furrows (as in *Nyssa*).

In a number of trees the bark exfoliates in definite layers (fig. 341), the separation being in a zone of weakness, known as the *separation layer*, which is composed of loose and weak cells that alternate with the denser and stronger cork layers. In trees with scaly bark the cork layers separate into patches or arcs (as in the sycamore, cherry, and pine), while in plants with ringed bark, the cork layers form concentric cylinders and the bark shreds or slivers off (as in the grape and arbor vitae). In trees with shaggy bark the exfoliating masses are elongated, and in the birches the bark exfoliates in thin, papery layers. In some trees the bark is supplemented in its protective rôle by dead-leaf bases (as in *Yucca*, p. 103).

The protective significance of different stem habits. — *Introductory remarks.* — The reproductive activity of stems appears to be exhibited somewhat equally in all situations, but foliage display is much more prominent in mesophytic than in xerophytic habitats, probably because the excessive transpiration in the latter makes it impossible for plants to develop greatly elongated stems; nor could plants with abundant foliage resist desiccation if such development were possible.

Tropical evergreen trees. — Only in the tropical rain forest is unrestricted foliage display observed, for there alone because of the lack of drought or cold is continued activity possible without protective structures or behavior. Daily synthesis and never failing moisture combine to produce the most luxuriant vegetation (fig. 152). An excellent example of the well-nigh perfect growth conditions of the rain forest is seen in the bamboo, whose stems sometimes grow as much as eight meters in a single month, or at a rate of more than twenty-five centimeters per day. However, the very excellence of tropical conditions causes such a superabundance of vegetation that only an occasional seed of any given species can fall in a place suitable for germination, and that only a few of the germinating plants can ever reach maturity.

Sclerophyllous evergreen trees.— Except in the rain forest, most trees are either deciduous or sclerophyllous (*i.e.* having stiff evergreen leaves), and must endure inclement seasons, characterized either by drought or by cold. In such regions trees have thick, impermeable

bark, and the leaves of sclerophyllous species are heavily cutinized and thus well protected against excessive transpiration (figs. 115, 263). The advantages possessed by such trees are extensive foliage display and the possibility of synthetic work at all seasons. However, there are corresponding disadvantages, since much energy and material are used in the construction of protective tissues, and since the heavily cutinized layers which reduce transpiration also reduce synthesis. Sclerophyllous evergreens may be broad-leaved, as in the olives, oaks, and hollies of warm temperate climates, or narrow-leaved, as in the conifers which have their culmination in cold climates.

Leafless evergreen trees. — Leafless trees, such as *Casuarina* and the taller cacti (fig. 342), are well fitted for climates in which all seasons are unfavorable, there being a relative minimum of synthetic surface and a relative maximum of protection from excessive transpiration, because of verticality, leaflessness, water accumulation, a highly cutinized epidermis, and slight surface exposure in proportion to volume. Restriction in foliage display, and hence in synthesis, generally is disadvantageous, but in arid regions it is of marked advantage since excessive transpiration entails far greater danger than does a scanty food supply. The cactoid form is illustrated not alone by the cacti of American deserts, but also by wholly unrelated plants of African deserts having almost identical form (*e.g. Euphorbia* and *Stapelia*). The four evergreen habits above noted, namely, rain forest evergreens, broad sclerophylls, narrow sclerophylls, and leafless evergreens, are fitted in the order mentioned for conditions that are increasingly xerophytic. Evergreen shrubs may be divided into the same four classes although the shrubs in each class extend into much severer climates than do the trees.

Deciduous trees. — Different as are the classes of evergreens and the conditions for which they are fitted, they agree in not changing their aspect from season to season. Deciduous trees (figs. 149–151, 264) and shrubs, on the other hand, exhibit leaf abscission at the inception of dry or cold periods, thus presenting two seasonal aspects. Such trees in the vegetative period may have leaves that are as expanded and about as little protected as are those of rain forest evergreens, while in the inclement period they are as well protected as are the cacti and better protected than are the sclerophylls. The obvious advantages of the deciduous habit are partially offset by obvious disadvantages; considerable energy and material are utilized in the development of

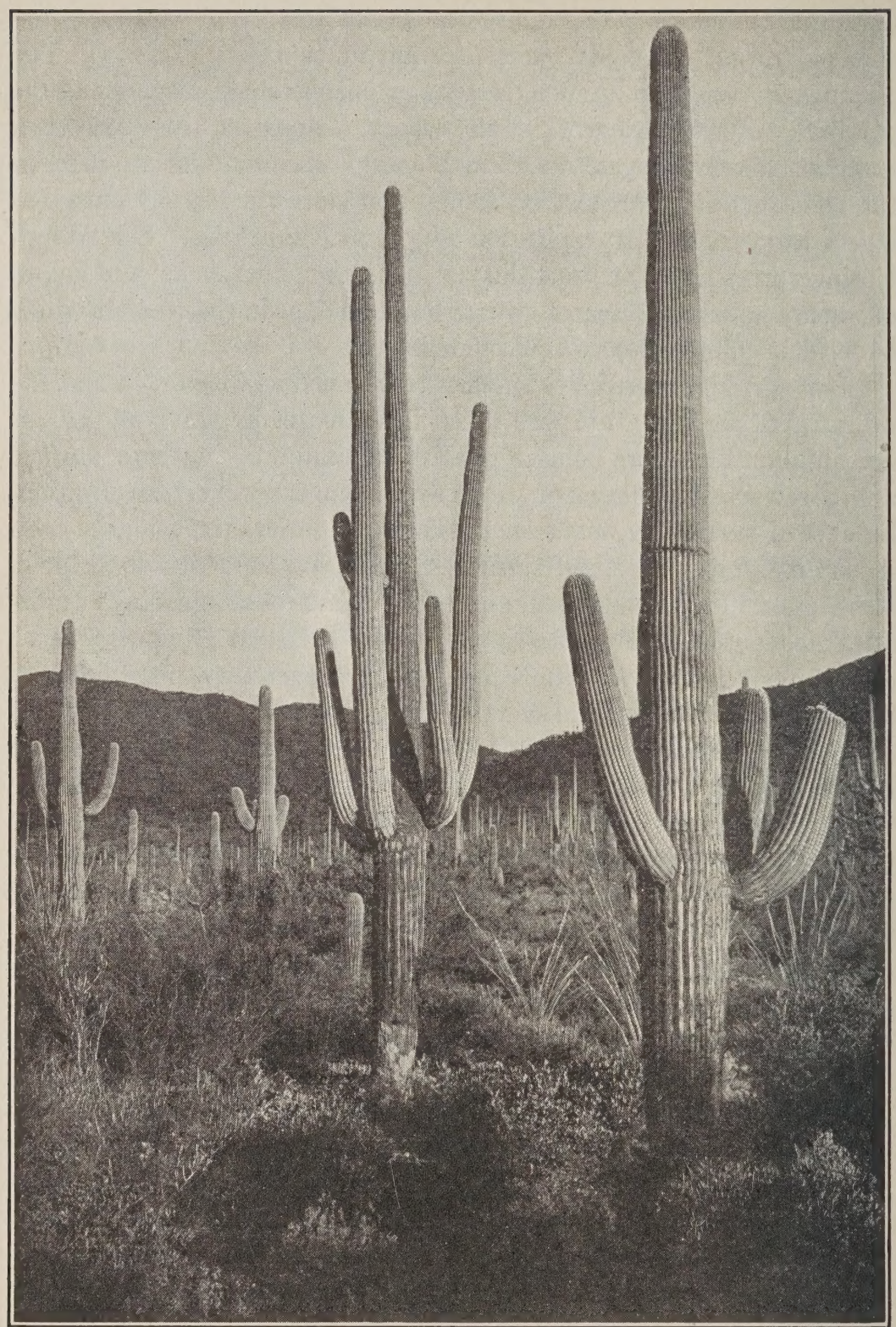


FIG. 342. — The giant cactus (*Cereus giganteus*), whose large and leafless vertical stems contain great quantities of water; note the prominent fluting of the stems; mountains near Tucson, Ariz. — From MACDOUGAL (Courtesy of the Carnegie Institution of Washington).

protective tissues and in complete leaf renewal each year; also deciduous trees are inferior to sclerophylls in the amount of synthetic activity on favorable days during the leafless period and in leaf protection on unfavorable days during the period of leafage.

Evergreen herbs. — Many herbs, especially in the tropical rain forest, are, like the trees, evergreen, presenting the same aspect at all seasons. There are some such plants, even in periodic climates, as the scouring rush (*Equisetum hyemale*, figs. 361, 362) and the prickly pear (*Opuntia*, figs. 347–349), which are leafless evergreen herbs well-fitted to withstand exposure. Also there is a large class of low herbs with sclerophyllous evergreen leaves, as *Linnaea*, *Mitchella*, *Cornus canadensis*, and the wintergreens (*Pyrola*, *Gaultheria*, *Chimaphila*). Another class of herbaceous evergreens includes forms which, at least in winter, are without aerial stems (as *Hepatica*, *Mitella*, *Geum*, and *Polystichum*); in this group are a number of species with relatively mesophytic leaves which readily survive the winter if transpiration is prevented by coverings of leaves or snow. Some herbaceous evergreens are more xerophytic, occurring in exposed situations (as *Artemisia*, *Taraxacum*, *Lepidium*, and *Oenothera*, fig. 343); when such plants are not protected by coverings of leaves or snow, many of the outer leaves die, but the younger leaves within are uninjured. Most of the xerophytic evergreen herbs and shrubs of cold climates form ground rosettes or have prostrate stems, and in many cases the aerial organs are arranged in cushions (fig. 367); in all such cases closeness to the ground or to other organs reduces transpiration and lessens the detrimental effect of sudden changes of temperature. Among the evergreen herbs should be classed most of the lichens, liverworts, and mosses, their small size often insuring sufficient winter protection by snow and leaves; furthermore, most lichens and many mosses are quite unharmed by months of exposure to transpiration without absorption. Such plants as the melon cacti (*Echinocactus*, fig. 370) may be regarded as evergreen herbs which are the extreme antithesis of tropical evergreen trees, having, on account of their spherical shape, the least possible transpiring surface in proportion to volume, and therefore illustrating the culmination of protective form among aerial organs.

Deciduous herbs. — In the great mass of herbs, particularly in periodic climates, aerial stems as well as leaves die at the inception of the unfavorable season. The death of the stem is not, as in the case of the leaves of woody plants, associated with a definite process of

abscission (except rarely, as in *Polygonatum*, fig. 291), but the death of the stem, even more definitely than that of the leaf, is occasioned by exposure to severe conditions. Only such parts survive as are in or near the soil. In *stem fall*, as it may be called, the stem gradually rots or weakens and falls to the ground and thus is comparable to leaf fall in ferns or in such trees as the beech and many oaks, where death ensues without the development of a well-defined absciss layer. In periods of drought, transpiration becomes too great to permit the survival of most aerial herbaceous stems, and in periods of cold also, transpiration becomes relatively excessive in proportion to the reduced rate of absorption. Aerial organs may die also as a direct result of freezing, though many plants, especially in alpine and arctic regions, are quite uninjured thereby, partly, perhaps, because of obviously protective structures, but more because of low water content, high osmotic pressure, or other and mostly unknown features. Tropical plants, on the other hand, may suffer injury or even death before the temperature reaches the freezing point of water. Many stems die in summer, even when the water supply is adequate; sometimes such death is attributed to old age, but old age is hardly a cause of death, being rather a result of certain causes, as yet imperfectly understood.

Perennial deciduous herbs. — In many perennial herbs essentially all stem organs are aerial, the perennating portions being just above the soil, as in *Lechea*, *Satureja glabra* (fig. 293), and *Linaria canadensis;* in these plants lateral shoots arise at the base of the erect stem and develop into short runners that remain over winter, while the erect stem dies. In many runner plants, as *Fragaria*, *Hydrocotyle* (fig. 13), and *Trifolium repens*, there are no prominent erect stems, the summer and the winter conditions thus being essentially alike. An herbaceous group with more numerous representatives is that in which the perennating organ is a multicipital stem (as in the dock and the dandelion, fig. 303); here the stem seems to disappear completely, the basal lateral shoots remaining embryonic through the inclement season. The majority of herbs in periodic climates perennate by means of underground organs, thus disappearing from view during the season of inactivity; the erect stem dies to the ground line or lower, and the stem is represented only by the rhizome (figs. 286–289, 291), tuber (figs. 297, 298), bulb (fig. 299), or corm (fig. 301).

Annuals and biennials. — The plants hitherto considered may be placed in three general classes: those with uniform seasonal aspect;

those in which the leaves are shed at the inception of the period of drought or cold; and those in which all aerial portions are lost at the beginning of the inclement season. The fourth and final class of land plants is that in which the entire plant dies at the inception of the inclement season. The most representative members of this class are the annuals, which are plants that live only in the favorable season, and which have fewer protective structures than do other plants. The annual alone among plants remains through seasons of severity solely

FIG. 343. — Winter rosettes of an evening primose (*Oenothera*), with leaves closely appressed to the ground; note the small amount of leaf overlap, due to high-ranked phyllotaxy and to variation in leaf length; Chicago, Ill. — Photograph by LAND.

in the form of its progeny, the seed. Related to the annuals are the biennials, which are plants that live in two vegetative seasons. In the first season most biennials develop a rosette (as in the evening primrose, peppergrass, and mullein, figs. 343, 146), which remains as such through the period of drought or cold. During the second vegetative season an erect shoot commonly appears and develops flowers and fruits, death ensuing at the inception of the second inclement period.

Annuals and biennials do not perennate, because they fail to develop lateral basal shoots; occasionally, however, some individuals of species that are classed as biennials develop such shoots and become triennials

or even quadrennials (as in *Artemisia canadensis*, *Arabis lyrata*, and some mutants of *Oenothera lamarckiana*, figs. 17, 18). Plants that are annuals in cold climates may be perennials in the tropics (*e.g.* the castor bean), and it is possible to cultivate some annuals or biennials as perennials by exposing them to favorable conditions during periods of severity (as in the pansy). Many annuals and biennials die relatively early in the vegetative season; for example, the staminate plants of the hemp (*Cannabis sativa*) die in late summer, while the pistillate plants with the developing seeds still are green and in full vigor. Indeed, most annuals and biennials that fruit early in the season die soon thereafter. The causes of such phenomena are unknown.

Aquatic herbs. — In the water the protective habits of many plants are comparable to those of the land, especially in such as have rhizomes, but unattached water plants form a class by themselves. Such floating plants, which include numerous large and small algae and some ferns and seed plants, are among the best protected of plants. The winter buds or shoots sink in autumn and rise in spring, thus requiring no such utilization of energy and material as in the deep placement of rhizomes and in the subsequent emergence of erect shoots. The chief disadvantages inhering in aquatic habitats arise from the instability of the water which makes impossible the growth of tall aerial organs and from its high refrangibility, which permits only moderate synthetic activity in submersed organs.

The compensatory relations of plant habits. — *General remarks.* — In the preceding paragraphs, reference has been made to the advantages and disadvantages of the various classes of plant habits, and it may be desirable, partly by way of summary, to contrast them further. In general, the principle of compensation is illustrated, disadvantages being offset by corresponding advantages. Erect and branching stems, whose habit well suits them for optimum display, are poorly suited for vegetative reproduction, and the construction of their protective tissues requires a great consumption of energy and material. On the other hand, horizontal ground stems, which are well suited for vegetative reproduction and which are protected with a minimum consumption of material, are unsuited for optimum foliage display.

Annuals. — Annuals as a rule are without conspicuous protective structures; this is not a disadvantage, because the non-existence of these forms during periods of severity makes protective tissues unnecessary for their optimum development. Thus an obvious advantage of

these plants is that all their energy and material are consumed in the development of organs directly concerned with nutrition and reproduction. A great disadvantage of the annual habit arises from the necessity that the entire race start anew from seed each year; thus the shortness of the season excludes annuals from alpine and arctic regions, and maximum foliage display is impossible for such forms in any region. Probably their chief disadvantage is that ultimately they are excluded from most habitats by perennials, owing to the increasing preëmption of ground by the perennating organs of the latter. Annuals reach their culmination in open situations, as in deserts and in cultivated fields, and along shores and roadsides.

Ground perennials. — Plants whose perennating organs are rhizomes, bulbs, corms, tubers, runners, rosettes, or multicipital stems may be termed ground perennials; such plants have a high measure of protection with a minimum utilization of structural material. The deeper the organ, the more complete is its protection from cold or transpiration, while the shallower the organ, the less is the amount of material consumed in reaching the surface at the inception of the growing season. Rhizome and runner plants surpass all other land plants from the standpoint of vegetative propagation, and bulbs, tubers, and corms are especially advantageous by reason of their abundant food supply, which facilitates the rapid development of aerial organs. Rosettes and multicipital stems have similar advantages, if the roots contain abundant food (as in the dandelion and the dock), though such habits are poorly suited for vegetative reproduction. Because the new shoots each year arise from the soil level or below, ground perennials, like annuals, are unable to display a maximum amount of foliage. However, rhizome perennials have about the most advantageous of plant habits, since they exhibit the combination of an enduring horizontal stem with a periodic erect stem; such a combination results in maximum protection with a minimum utilization of structual material, in maximum reproduction, and in adequate, though minor, foliage display. Plants with bulbs, tubers, or corms are suited especially for districts with short vegetative periods, as the Mediterranean region, where the winter is too cold and the summer too dry for optimum growth activity, the most favorable seasons being periods of short duration in the spring and autumn; in these plants much of the food utilized in a season's growth is accumulated the year previous, and is ready for almost instant use upon the arrival of favorable conditions.

Trees and shrubs. — Trees and shrubs utilize a large amount of energy and constructive material in the development of a protective bark and of a mechanical skeleton, and they are at a disadvantage in the matter of vegetative reproduction. However, growth resumption at the point of growth cessation the year previous makes possible an optimum display of foliage. Trees and shrubs are fitted for all climates where there is an adequate supply of available water. In deserts tree development is slight, because of constant and extreme exposure to excessive transpiration together with limited absorption; shrubs, however, often are abundant in arid climates. In alpine and arctic regions there is sufficient moisture, but its unavailability through the long winter makes life conditions severe for trees, on account of continued transpiration; shrubs are more fully developed, because they are better protected during the winter. There are no places too cold for trees, if sufficiently protected from transpiration. Trees are absent from many alpine and arctic habitats where snow lies on the ground for most of the summer, but the most extensive treeless tracts are the prairies, where it is probable that a combination of inadequate rainfall and excessive winter transpiration best accounts for the absence of trees.

The duration of stems. — At one extreme as to duration are ephemeral annuals that live but a few weeks or even days, and at the other extreme are trees whose life may be measured by centuries. Annual aerial stems occur not alone in annuals, but also in most biennials and in most herbaceous perennials of periodic climates. Most bulbs and tubers live but a year or two, the old organ dying upon the development of new bulbs or tubers. Of somewhat longer life, but still relatively short-lived, are various rhizomes, which advance anteriorly each year, while dying posteriorly, a given portion commonly enduring for a few years. Trees and shrubs remain alive much longer, appearing to have a more or less definite period of life, varying with the species. While in some cases a trunk may endure for a number of centuries, any given part lives but a few years, namely, for the length of time elapsing before the sap-wood becomes transformed into heart-wood; in many trees the dead heartwood resists decay for centuries.

Roots commonly equal or surpass stems in the matter of duration. The stems of annuals and of most trees and shrubs and the underground stems of perennial herbs commonly are as long-lived as are the roots, but the stems of biennials,

the aerial stems of perennial herbs, and the trunks of shrubs and trees that develop basal suckers usually are shorter lived than are the roots; while the trunks of the redwood live for centuries, the roots might live indefinitely. Little is known concerning the causes of varying duration. In trees the continued decay of the heartwood may be a factor, and perhaps the increasing distance year by year between the root tips and the upper branches may involve a decreasing water supply.

6. THE ACCUMULATION IN STEMS OF WATER, FOOD, AND WASTE PRODUCTS

Introductory remarks. — Plants often are supposed to store food or water, which they or their progeny utilize later, much as men and animals store food for winter use. Such a conception appears to involve forethought, and should be discarded.[1] A better conception is that unused material accumulates. If a plant manufactures more carbohydrate or protein than it utilizes, or if it takes in more water than it utilizes or gives off, the residue necessarily accumulates. Sometimes such surplus food and water are subsequently utilized, but at other times they remain unused. In the latter event they differ from ordinary waste products only in that they are capable of use in constructive metabolism.

The accumulation of air and water. — Stems, as well as leaves, are characterized by air spaces and air passages and sometimes by capacious air chambers, especially in such hydrophytes as *Myriophyllum* (fig. 94), *Hippuris*, and *Hottonia;* the oxygen and carbon dioxide contained herein may be of especial advantage to submersed hydrophytes, if their gas supply is otherwise deficient. In some cases stem air spaces assist in flotation (as in *Hottonia*). Water accumulation, which has been discussed in connection with leaves, is a conspicuous phenomenon also in stems, notably in deserts. The most remarkable cases of water accumulation are in the cacti and in plants of similar form (as *Euphorbia*, *Stapelia*, and *Cavanillesia*, the latter having barrel-shaped trunks); such habits are advantageous, because of the small transpiring surface in proportion to the stem volume (figs. 342, 347–349). During rainy periods the stems accumulate large quantities of water, which become depleted during subsequent drought. The fluted stem of the giant cactus (fig. 342) undergoes accordion-like expansions and contractions during wet and dry periods respectively, the maximum circumferential difference being considerable. Many

[1] The term, *reserve food*, is similarly objectionable, since it directly expresses forethought; a preferable expression is *surplus food*.

plants outside of arid regions have fleshy stems, as *Portulaca* and *Begonia*, and succulence is a notable feature of many halophytes, as *Salicornia*. Many underground stems accumulate water, as well as food, in large amount; this is true especially of tubers and corms.

The accumulation of foods. — *General remarks.* — In sunshine most leaves manufacture more food than is disposed of during the day, this excess commonly accumulating as starch. During the night, when carbohydrate manufacture ceases, this starch is transformed into sugar and migrates to other parts of the plant. Food accumulations of much greater permanence occur in stems, roots, and seeds, because the manufacture of food is more rapid than is its use in growth or otherwise.

Food accumulation in aerial and aquatic stems. — In trees and shrubs, food accumulates, especially in the cortex, medullary rays, and wood parenchyma, and in some instances even in the central pith region (medulla). The carbohydrates that accumulate in the trunk may assume various forms, starch on the whole being the most representative. In most trees, shrubs, and evergreen herbs of temperate and cold climates, there is in autumn a maximum of starch, which accumulates chiefly in the parenchyma. Since low temperatures favor the conversion of starch into sugar, the latter then increases at the expense of the former; it is believed that this sugar is of protective value (p. 103). In early spring the sugar moves toward the buds, and again is transformed into starch, which accumulates especially in the embryonic leaves.

In some trees carbohydrates are transformed into fats at the inception of winter, while the reverse transformation takes place in spring; among the trees that accumulate fats are such northern trees as birches and conifers, and it has been supposed that these fats are of protective significance during periods of low temperature. Sometimes there is developed in autumn in living leptome and wood cells a *hemicellulose* layer which is dissolved the following spring. In herbaceous stems the cortex and bundle sheath frequently are regions of starch accumulation, especially in water plants (fig. 324).

Food accumulation in subterranean stems. — The chief subterranean stem organs of food accumulation are tubers and corms (figs. 297, 298, 301), in which the food commonly is starch that is formed by leucoplasts in the cells in which it accumulates. Sometimes the starch grains of underground stems are relatively large, as in the potato tuber (figs. 513, 514), and in the rhizome of *Canna*, where individual grains may be 0.17 mm. in length. The chief advantage associated with

corms and tubers is that their food supply enables them to renew activity speedily at the inception of a favorable period, a matter of much significance in climates like that of Italy, where short favorable periods are intercalated between long periods of inactivity.

The rôle of accumulated foods. — The plant that accumulates the food may itself utilize it; for example, during the vegetative season the trunks of deciduous trees gradually accumulate quantities of starch and other foods, which are utilized in the development of shoots the following spring; or the accumulated food may be utilized by vegetative offshoots, as in plants that give rise to bulbs and tubers. Again, the food accumulated in seeds may be used by the progeny of the accumulating plant. Finally, accumulated food may be used by a foreign organism or even remain unused. Non-utilization is more frequent then usually has been supposed. Most tubers and bulbs and some seeds contain more food than is used under ordinary conditions by the germinating plant, though it is probable that an excess beyond the amount necessary to support the plant until it reaches the light is beneficial in the way of giving it a "running start."

FIG. 344. — A tuber of the potato (*Solanum tuberosum*), which has germinated in a dark, moist cellar; note the wrinkling of the tuber, evidencing the withdrawal therefrom of food and water by the developing shoots.

In the potato tuber there is a large excess of food beyond the amount utilized in germination (fig. 344). In various orchids (as in *Neottia*) the amount of accumulated food which is utilized is small compared with that which is left; after a time such food decays and contributes to the humus. The large quantities of food accumulated in galls are valueless to the accumulating plants. Latex contains starch and other foods that never are utilized, so far as is known. During the summer and autumn there is a well-marked migration of food from the leaves to the trunk in deciduous trees; however, considerable food remains in the leaves at leaf fall and hence never is utilized.

The detailed consideration of the structure and arrangement of plant foods is deferred to the chapter dealing with seeds (p. 427).

Latex. — *The structural features of latex elements.* — A few plant families are characterized by the presence of milky juice, or *latex*. Genetically, latex elements are of three sorts, the simplest being the *latex sac*, where the milky juice is contained in uninucleate cells, usually arranged in longitudinal rows, as in *Sanguinaria*, and also in the Con

volvulaceae and Sapotaceae, the latter family including *Palaquium*, which furnishes the gutta percha of commerce. The second and commonest kind of latex tissue is that in which the cells fuse (as in tracheae) by the resorption of the connecting walls, thus forming syncytes known as *laticiferous vessels*, which form a connected cortical system throughout the plant (fig. 345). Sometimes the cells fuse in rows, as in the celandine poppy, thus forming an easy transition to rows of latex sacs. More commonly there is lateral as well as terminal fusion, resulting in an anastomosing network, as in the milky-juiced composites (Cichorieae); similar laticiferous vessels characterize the fungus *Lactarius*. The third and most extraordinary kind of laticiferous tissue is that characterizing *Euphorbia* and the milkweeds (Asclepiadaceae), where the laticiferous element is a coenocyte, arising in the embryo from a single ordinary cell. Later this develops at an equal rate with the plant, penetrating among the cells as do the hyphae of a parasitic fungus, and sometimes attaining a length of several meters; branching occurs freely, but the branches rarely anastomose. In all cases latex tissues occupy definite regions and traverse the entire plant, as do vascular tissues.

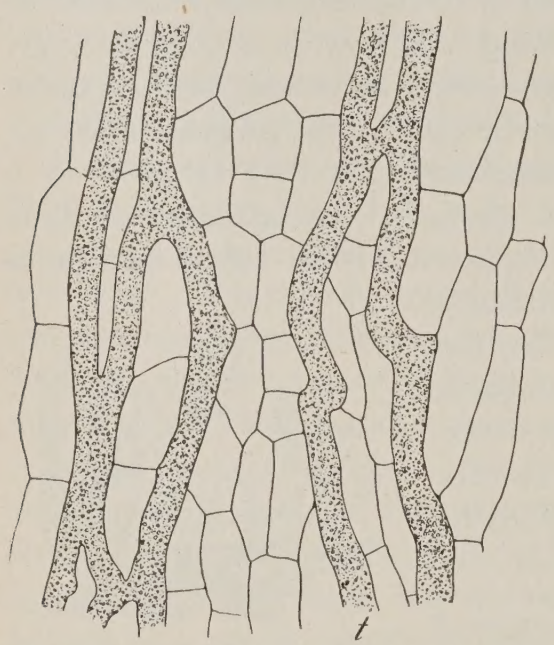


FIG. 345. — A longitudinal section through a portion of a root of the prickly lettuce (*Lactuca scariola*), showing the anastomosing latex tubes (*t*) note the absence of cross walls; highly magnified.

The contents of latex tubes. — Latex elements, whether they are cells, syncytes, or coenocytes, contain an extraordinary assemblage of substances. Latex consists of a watery fluid, which holds in suspension gums, resins, caoutchouc, fats, and waxes, and therefore is an emulsion; in addition there are held in solution tannins, soluble gums, sugars, alkaloids, salts, and occasionally proteolytic ferments (as papain in *Carica papaya*). *Leucoplasts*, *elaioplasts*, and *proteinoplasts* occur in the latex, organizing respectively starch grains, oil bodies, and protein granules; in *Euphorbia* there are starch grains of unusual

shape, resembling rods, dumb-bells, etc. As a rule latex is white, as suggested by the common name of milky juice, but in the poppy family it may be yellow, orange, or red. Latex elements are living, having thin plasmatic layers along the walls, which commonly are thin and readily permeable to water and solutes, though in *Euphorbia* the walls are thicker and pitted.

In many plants (as in the common milkweed, *Asclepias syriaca*) latex flows copiously from a wounded surface, indicating its great abundance and also the high pressure at which it exists in the tubes; it soon coagulates upon exposure to air. Latex is of great commercial value, as it is the chief source of rubber; the leading rubber-producing plants are tropical trees of the nettle, dogbane, and spurge families. Opium is a mixture of alkaloids from the latex of the poppy.

The rôle of latex. — The presence in latex of leucoplasts, proteinoplasts, and elaioplasts (together with the starch, protein, and oil which they form), as well as of proteolytic ferments, has led to the theory that latex tubes are food reservoirs; this theory finds further support in the fact that in rapidly growing young plants of *Euphorbia lathyris* the latex is very milky and is rich in starch, fats, and albuminous substances, while in old plants the latex is translucent and watery and is poor in these substances; furthermore, in winter, albumin is scarce in the stem latex and abundant in the root latex. Again, plants grown in the dark or in air that is deprived of carbon dioxide have weak watery latex without starch. However, the presence of such waste products as caoutchouc, gums, resins, waxes, tannins, and alkaloids has led equally to the theory that latex tubes are excretory reservoirs. The presence of starch does not necessarily favor the food reservoir theory, since there is little evidence that the starch is ever used; in starved plants, for example, it suffers no appreciable decrease. There is some evidence that the fats and proteins of latex are utilized as food. Very probably latex tubes are general catch-alls, containing both surplus foods and waste products; the latter generally are greater in amount, and it is likely that the latex tubes are of significance chiefly as excretory reservoirs.

Related to the food reservoir theory is the hypothesis that latex tubes represent a conductive system, a hypothesis favored supposedly by the continuity of the tubes and by the paucity of cross walls, as well as by the intimate connection sometimes existing between the ends of the tubes and the palisade cells. The adherents of the conduction theory regard the latex tubes as paths of movement of carbo-

hydrates and proteins; even starch grains are thought capable of movement herein, since they sometimes accumulate behind a wall or other obstruction, apparently as logs pile up in a jam. The conduction theory rests more on analogy than on experiment. Also related to the conduction and food reservoir theories is the hypothesis that latex tissue represents merely water tissue. Laticiferous plants usually are very succulent, and it is possible that some of the substances associated with water in latex have an effect similar to that of salts in halophytes in retarding evaporation. While many laticiferous plants grow in the rain forest, the majority, perhaps, are xerophytic, *Euphorbia* furnishing many notable examples; however, milky-juiced plants are not as strikingly xerophytic in distribution as are ordinary succulents.

Another theory as to latex is that its coagulability is advantageous in healing wounds, but this is no more a rôle of primary importance here than it is in blood, which behaves similarly. A final theory is that latex, because of its poisonous or at least unpalatable nature, protects plants from animals; mere contact with the milky juice of *Lactarius* is said to be fatal to snails, and it is conceivable that its general alkaloid content may make latex prejudicial to other animals. Many laticiferous plants, however, are favorite food plants for man and for grazing animals. Further experimentation is needed before the latex problem can be solved, and particularly experimentation bearing on the causes underlying the formation of latex and latex tubes. The presence of various kinds of plastids in latex tubes may indicate a high degree of independent nutritive activity in spite of the absence of chlorophyll.

The accumulation in stems of mucilage, oils, resins, crystals, tannins, and dyes. — *Ducts.* — Stems, as well as leaves, may contain crystals or be clothed with glandular hairs. In many stems there are *ducts* that secrete and accumulate resins, oils, or mucilage, all gradations existing, especially in conifers, between these structures and internal glands. Ducts originate as do internal glands, and their structural features are similar, the chief difference being that they are elongated in an axial direction, and are more or less continuous. In most cases there is a branched and anastomosing system of continuous ducts throughout the plant, though in pine needles the ducts end blindly. Often (as in the pine, fig. 346) the secreting cells are enclosed by a protective sheath of thick-walled cells, interrupted here and there by permeable transfusion cells. Mucilage ducts are characteristic of cycads and of many ferns, and oil or resin ducts characterize most conifers and many composites, as the rosin-weeds (*Silphium*). The mucilage tubes of certain liliaceous plants resemble latex tubes, not

alone in structure, but also in diversity of contents since they contain protein crystals, starch, tannin, and glucose; in addition they have remarkable filamentous nuclei. In some conifers, reservoirs filled with resin occur in the bark, as in the balsam blisters of the fir (*Abies balsamea*).

The rôle of duct secretions. — Probably the contents of resin and mucilage ducts are chiefly waste products. Since such substances usually cannot be excreted externally, it is presumably advantageous that they accumulate in reservoirs outside the regions of nutritive activity. Even if resins and similar excretions are waste products, they may have subsidiary advantages; for example, they may preserve the wood from decay, as in the conifers, thus facilitating longevity. Perhaps resins and gums are of advantage in healing wounds and in checking loss of water, as in the pines and cherries, where they exude copiously at the injured places. Incisions cause not only the flow of resin, but also in some cases the development of accessory ducts.

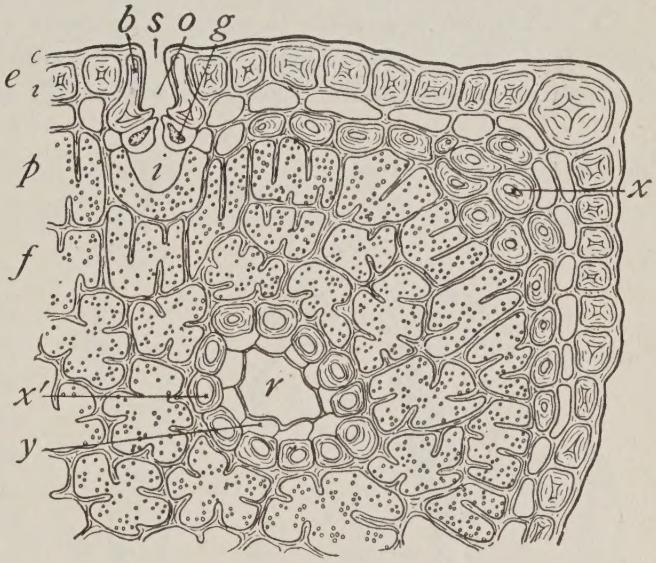
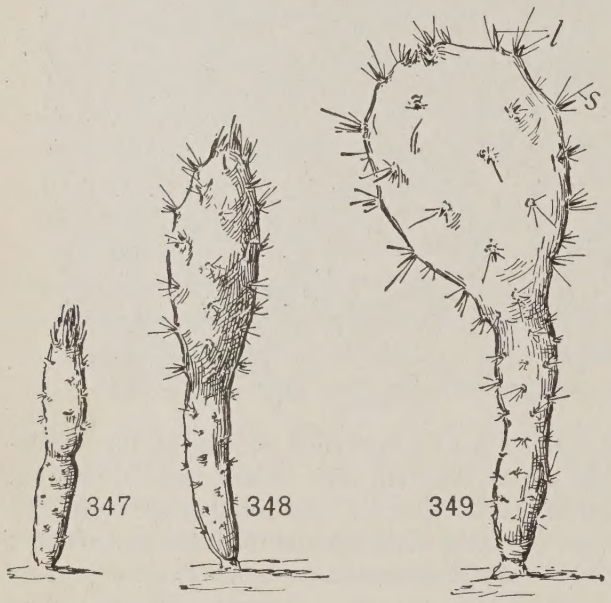


FIG. 346. — A cross section of an edge of the needle-like leaf of the Austrian pine (*Pinus laricio*), showing the epidermis (*e*) with its much thickened walls, the outer part (*c*) being cutinized and the inner part (*i*) not; *x*, hypodermal sclerenchymatous tissue *f*, chlorenchyma with infolded cell walls, the outermost cells (*p*) having these walls perpendicular to the surface, suggesting palisades; *s*, stoma with guard cells (*g*), subsidiary cells (*b*), stomatal cavity (*i*), and pit (*o*); *r*, resin duct, the secretory cells (*y*) being surrounded by a sclerenchymatous cylinder (*x'*); highly magnified.

Tannins and other bark excretions. — Among the commoner excretions found in bark (as in the oak) are *tannins*, which are astringent glucosides. In *Sambucus* the tannin is contained in special sacs, twenty millimeters long or thereabouts, but usually the tannin-containing cells are in rows and often near the vascular tract. Brown and red colors in the bark interior often are due to tannins. Similar to the tannins is *salicin*, which occasions the bitter taste of willow bark. Most tannins doubtless are waste products and eventually they are removed through the exfoliation of the bark; similarly, exfoliation rids trees of many other waste products that accumulate in the bark, such as alkaloids, gums, resins, and calcium oxalate.

Tannins, because of their bitterness, may be useful incidentally in protecting from animal depredations; some tannins, known as plastic tannins, probably are of value in nutrition. Tannin production appears to be especially characteristic of xerophytes; desert plants growing in mesophytic conditions have much less tannin than in their natural habitat. In *Jussiaea*, tannin formation has been shown to be favored by exposure to dry air and to light.

The accumulation of waste in wood. — In many trees the heartwood serves as a reservoir of various excreta which may give it a color different from that of the sapwood, as in the red cedar (*Juniperus virginiana*) and in the black walnut. The colored heartwood usually is much harder than the white sapwood (as in mahogany and ebony), whence the significance of the name *duramen*. Occasionally the medulla is a reservoir of excreta, as in the sumac, where it is colored yellow. Doubtless the chief advantage of the accumulation of such substances in the duramen is that thus they are removed from the active tissues, though it is an important subsidiary advantage that they increase the durability of the heartwood and thus promote longevity.



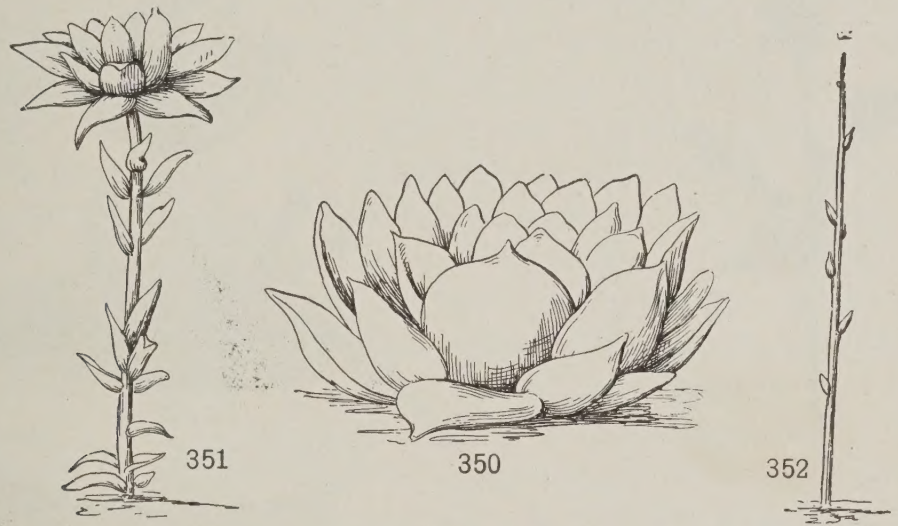
FIGS. 347–349. — Young plants of a prickly pear cactus (*Opuntia rafinesquii*), showing the ontogenetic differentiation of a flattened stem from a cylindrical "juvenile" stem: 347, a very young plant with a cylindrical stem, showing the product of two growth periods; 348, an older plant in which the second segment, although cylindrical, is much broader than the first; 349, a still older plant in which the third segment has the flattened form characteristic of "adult" individuals of the genus; the small and soon deciduous leaves (*l*) bear spines (*s*) in their axils.

7. VARIATION IN STEM FORM

Elongation in aerial stems. — *Variation in tree form.* — Forest individuals of most trees differ widely in form from individuals grown in the open, the trunks of the former being tall and slender, while those of the latter are short and stout. Furthermore, trees in the open are profusely branched, even near the base, whereas in forest individuals the branches at the lower levels soon die and fall to the ground, leaving the tree relatively unbranched except near the top. Many herbs show comparable phenomena, isolated individuals being relatively short, stout, and branched, and crowded individuals relatively tall, slender, and unbranched; in dense cultures the lower leaves die much sooner

than on isolated individuals. The death of the lower leaves in crowded cultures, and probably the death of the lower branches of trees in the forest, is due to insufficient light; if a forest tree is left standing when its neighbors are cut, the trunk often develops adventitious leafy shoots in great abundance, probably because it is more exposed to light. In various trees (*e.g.* willows and poplars) there occurs "self-pruning," or *branch fall*, that is not readily referable to definite factors.

Light as a factor in elongation. — The causes of elongation in crowded cultures are not certainly established, though they are clearly external.



FIGS. 350–352. — Stem and leaf variation in *Sempervivum assimile:* 350, a stemless rosette, as seen in nature, having imbricated leaves in many ranks; 351, an individual that has been grown in a moist chamber; note the conspicuous erect stem with its terminal rosette; 352, an individual that has been grown in a moist dark chamber; note the small and scattered leaves. — After BRENNER.

Sometimes the differences to be accounted for are very great, as in the palmetto, which in dry open habitats often is stemless above ground, while in moist woods, plants of equal age have long, slender trunks several meters in height. When the prickly pear (*Opuntia*) grows in the light, the stems become much flattened (fig. 349), while in darkness they become slender, elongated cylinders, somewhat comparable to their "juvenile" stems (figs. 347, 348). The stems of *Genista* develop flattened wings in the light but not in darkness. In germinating potato tubers, slender elongated stems issue from buds located below the soil level, while short and very stout shoots may issue from buds above ground (fig. 353). The stipes of *Mucor* and *Coprinus* elongate in the darkness and are relatively short and stout in the light.

These and similar facts have led to the view that light retards, and that darkness favors elongation.

Moisture as a factor in elongation. — Certain of the Crassulaceae (notably *Sempervivum assimile*, fig. 350) usually are stemless in their natural xerophytic habitats, while growth in moist, light chambers results in the conspicuous development of erect leafy stems (fig. 351); growth in moist, dark chambers results similarly, except that leaf formation is greatly reduced (fig. 352). These and many similar ex-

FIG. 353. — A potato plant (*Solanum tuberosum*), grown from a tuber planted with one end in the soil, but with the larger portion in the air; note the short and stout aerial shoots, which contrast strikingly with the long and slender shoot which originated in the soil; note also the much larger leaves on the latter shoot. — Photograph by FULLER.

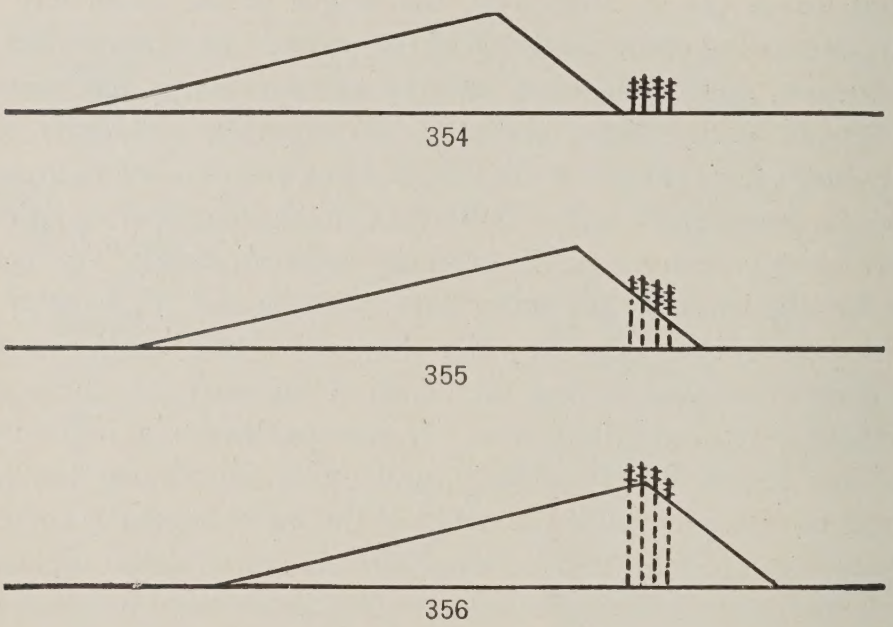
periments show conclusively that moisture favors elongation, while desiccation results in shortened and often in laterally enlarged stems; as might be expected, the presence of soluble salts in the culture media produces the same effect as desiccation. There are few if any similarly conclusive experiments as to light, and it seems probable that moisture differences constitute the chief factors in determining the phenomena noted in the preceding paragraphs. Indeed, in some cases (as in *Jussiaea* and in the seedlings of *Vicia faba*) there is greater elongation in illuminated than in dark cultures, if the moisture conditions are equal and favorable. Stem internodes become shorter and thicker and the plant more bushy, if the ordinary supply of carbon dioxide is

doubled or quadrupled, but in nature this factor is not likely to be important. Variations in the length of petioles, as in the maple (fig. 82), doubtless are due to the same cause as are variations in the length of stems, that is, to differential shading or more probably to moisture differences due to differential shading. For a consideration of the striking elongation of pendulous stems, see p. 173.

Elongation in aquatic stems and petioles. — *The phenomena.* — In water plants with floating leaves (as in *Polygonum amphibium*) or with emersed leaves (as in *Hippuris*), the length of the stem may vary widely, depending upon the depth of the water. In swamps that have been flooded, stem elongation may be extraordinary, ten times the usual length having been reported; for example, *Eleocharis* stems, usually but a few centimeters in length, have been known to grow to a length of a meter and a half. Differences in the length of aquatic petioles are more common, and if anything more striking. The petioles of the floating leaves of the water lilies, *Castalia* and *Nymphaea*, vary with the depth of the water in which they grow, their length commonly being somewhat greater than the depth of the water, a phenomenon that results in oblique orientation. In emersed leaves (as in *Sagittaria*) the petiole length varies similarly, and under experiment the leaves continue to emerge, even if the depth of the water is greatly increased. Elongated water stems and petioles, like elongated aerial organs, are very slender, so that an increased amount of structural material is not necessarily involved in elongation. As might be expected, it is possible experimentally to find a depth too great for the elongating petiole to raise its blade into the air.

The probable factors. — The striking fact in hydrophytes with floating leaves is not so much the varying length of stems and petioles as the cessation of growth at the water line, as though at that level some new factor came suddenly into activity. Such a factor, of course, is transpiration, and it seems probable that this is the chief factor involved in such cases, since growth in covered aquaria, where transpiration is greatly reduced, results in the development of emersed leaves in place of floating leaves in *Hydrocharis*, *Nymphaea*, and *Potamogeton natans*. Short aerial stems and petioles as compared with the corresponding elongated aquatic organs also would seem adequately accounted for by differences in transpiration. Variations in oxygen content sometimes have been thought to explain differential elongation in aquatic stems, though it is not easy to see why a stem

should grow longest where the oxygen supply is smallest, nor why there should be a sudden arrest of growth at the water line. Similarly, differences in light intensity often are cited as factors in the elongation of aquatic stems as well as of aerial stems. While diminished light might cause elongation in deep water, the increase of light in passing from water to air is not sufficiently sudden to account for the arrest of growth at the water line. The failure of deeply submersed leaves to reach the surface may be due to diminished synthesis, and thus indi-



FIGS. 354–356. — Diagrams showing the stem elongation of certain plants (as willows or dogwoods) when submerged by advancing sand dunes; 354, a dune in whose path of advance is a swamp with such shrubs of ordinary height; 355, the same place a few years later, the dune having advanced; note that the stems of the shrubs have twice their usual length; 356, the same place, after the lapse of a few more years; the stems of the shrubs have four times their usual length.

rectly to light. The mechanical support given by water occasionally has been thought to have some connection with the great elongation in that medium.

Elongation in stems submerged by sand. — *The phenomena.* — Still more remarkable than the elongation of aquatic stems is the elongation exhibited by certain aerial stems that are partially buried by the sand of moving dunes. While some trees (as oaks and pines) soon succumb to the sand, others (as the white elm and the red maple) remain alive for years, unless completely covered. A number of trees and shrubs, notably willows (as *Salix syrticola* and *S. glaucophylla*), dogwoods (as *Cornus stolonifera*), and poplars (as *Populus deltoides*), not only remain alive, but are stimulated to a growth far exceeding that of ordinary aerial stems. Dogwoods and willows, which in ordinary habitats rarely attain a height of more than

two or three meters, may have stems twelve, fifteen, or even eighteen meters above the original ground level, if partially submerged by sand (figs. 354–356). The growing stems usually keep pace with the rising sand, so that the height above the ground remains about the same year after year, approximately equaling the usual height of the shrubs.

The possible factors. — While the exact factors determining elongation in partially buried stems are not clearly known, it is significant that only those stems exhibit elongation which develop adventitious roots in the moist sand (fig. 357). Some trees (as the red cedar) ordinarily are of low stature, while other trees (as the eucalyptus) are very tall; the factors determining the potential height of the stem in various species are quite unknown. Increasing height probably is accompanied by accelerated transpiration, and an increasing root system makes possible increased absorption. It is likely, however, that the transpiration increase gradually exceeds the increase of available water, owing to the conjunction of increased transpiring surface, increased exposure to transpiration, and increased length of the conductive tract; ultimately the available water may be sufficient merely to make good the loss by transpiration, leaving no surplus for elongation. This condition, ultimately reached in all trees, may be reached much sooner in some species than in others, owing to peculiarities of structure and behavior. If this hypothesis is valid, stem elongation in dune sand may be explained by the fact that the absorptive system increases as fast as the transpiration is accelerated; the distance traversed by water in reaching the topmost organs remains essentially the same, since the adventitious roots keep pace in their development with the increasing elongation of the stem.

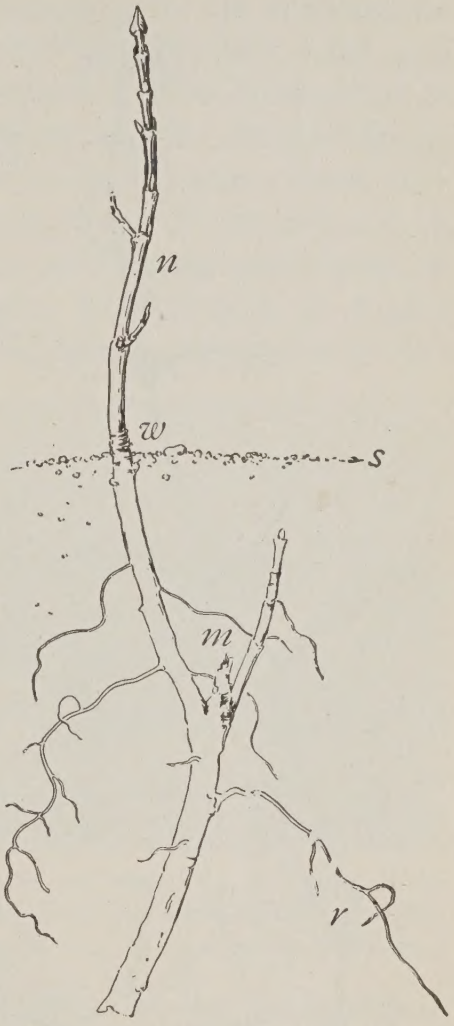


FIG. 357. — The apical portion of a plant of the red-osier dogwood (*Cornus stolonifera*) that has been almost buried by dune sand; note the adventitious roots (*r*) that have issued from the stem; the main shoot (*m*) has been killed, but one of the lateral shoots (*n*) still keeps above the sand; note that the scars (*w*) left by the falling of the scales of the previous winter bud are at the sand line (*s*), showing that the plant was almost completely buried.

Stem dwarfing. — *Alpine and lowland cultures.* — Alpine stems commonly are dwarf, and, if much-branched, they are compact and bushy, often forming dense mats or cushions. In some very careful experi-

ments both alpine and lowland individuals of many species were split into two parts, one of which was grown in an alpine garden, and the other in the lowlands; the portions taken from alpine districts to low altitudes developed slender elongated stems, while the portions taken from the lowlands to the mountains developed short and stout stems, the whole aerial system assuming a bushy and compact habit. The leaves and flower stalks, as well as the stems, underwent reduction (figs. 358, 359, 175, 176). Hence alpine conditions are thought to account for the prevalent habits of alpine plants.

FIGS. 358, 359. — Leaf and stem variation in *Helianthemum vulgare:* 358, an individual grown in a lowland garden, showing elongated stems and relatively large leaves; 359, an individual grown in an alpine garden from a part of the same plant from which 358 was taken; note the numerous dwarfed branches with their much smaller leaves and but slightly smaller flowers; *b*, bracts; *x*, calyx; *c*, corolla; both figures equally reduced. — After BONNIER.

Krummholz. — The mountain pine of Europe (*Pinus montana*) in the Alps is a gnarled and sprawling, much branched shrub, but when grown in the lowlands it is a tree much like other pines. German botanists use their com-

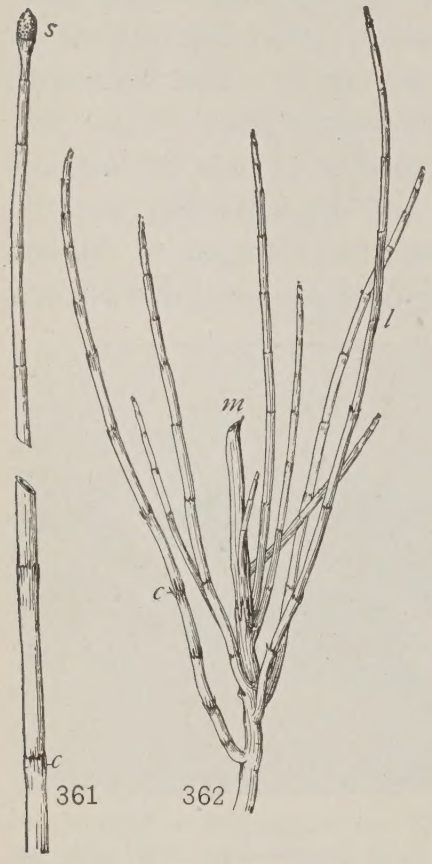
mon name for this plant, *Krummholz* (gnarled wood), as a general term for the scrubby growth of woody plants above the timber on mountains, and for lack of a suitable English term, the word may be employed here. On most mountains the "timber line" trees pass gradually upward into a scraggy *Krummholz;* good illustrations of this habit are afforded by the spruce (*Picea*) and fir (*Abies balsamea*) on the New England mountains, the white-barked pine (*Pinus albicaulis*) on the Rocky Mountains, the foxtail pine (*Pinus aristata*) on the San Francisco Mountains of Arizona, and the mountain hemlock (*Tsuga mertensiana*) on many mountains from Oregon to Alaska (fig. 360). In many alpine regions dwarfed alders, willows, and birches

FIG. 360. — Alpine *Krummholz*, made up of gnarled and weather-beaten trees of the mountain hemlock (*Tsuga mertensiana*); note that the living branches bend down and trail over the ground, forming a dense tangle; Mount Hood, Ore. — Photograph by MEYERS.

mingle with the conifers. The impenetrability of the *Krummholz* is due in part to the multiplicity of scraggy lateral branches, but more to the fact that these branches bend down close to the ground and twist and turn in all directions.

The determining factors of the Krummholz. — The factors determining the *Krummholz* probably are complex, though not as yet adequately tested by experiment. Probably the short, thick growth of the stems is due chiefly to relatively high transpiration in proportion to absorption, absorption being reduced because of the dryness and the low temperature of the soil, while the transpiration often is accelerated because of strong winds, atmospheric rarity, intense sunlight, and low humidity. The multiplicity of branching is due to the replacement of the terminal shoots by numerous lateral shoots, as soon as the former reach a height where the excessive transpiration makes

further growth impossible; a prominent factor here is the depth of winter snow, since branches above the snow level are exposed to transpiration for many months during which there is no absorption. Here, as elsewhere, the destruction of the terminal shoot is followed by the development of many lateral branches, whose subsequent destruction results in a still greater number of new laterals, and so on, until there is at last an inextricable tangle of branches. The tortuous descending branches so characteristic of alpine conifers probably are associated with severe mechanical factors, such as strong winds, the weight of the winter snow, and snowslides. Even below the "timber line," tree trunks sometimes bend down-hill at the base, owing to the weight of snow borne by the plant when it was a young and flexible sapling.



FIGS. 361, 362. — Stem variation in the scouring rush (*Equisetum hyemale*): 361, an erect, unbranched stem, terminated by a strobilus (*s*), being the form commonly seen in protected situations; 362, a much-branched stem from an exposed sand dune; following an injury to the terminal shoot (*m*) there has been conspicuous regeneration, a number of latent buds having given rise to lateral branches (*l*); note the absence of foliage leaves; *c*, scale leaves.

Arctic dwarfs. — The polar regions, like the mountain tops, are characterized by dwarf vegetation, composed largely of cushion herbs, rosette herbs, mat-forming plants, and *Krummholz*. The *Krummholz* is made up largely of dwarfed specimens of woody plants (*e.g.* larch, spruce, and birch) which in more genial climates develop into trees. While not experimentally attested, it is likely that the factors involved are similar to those that are supposed to obtain on mountains; transpiration, perhaps, is less than in alpine regions, on account of the less intense light and the greater atmospheric pressure, but absorption also is less, because the soil is more constantly cold.

Dwarfing in arid situations. — Xerophytic vegetation, such as that of dry rocks and sand, often is dwarf, though much less so than that of alpine and arctic regions, and the dwarfness is less clearly due to the surrounding conditions. The stem of *Equisetum hyemale*, which commonly is unbranched in mesophytic and swampy habitats, often is much branched in dry, exposed situations, the destruction of the terminal shoot by excessive transpiration or otherwise being followed by a strong development of lateral branches, as in the

Krummholz (figs. 361, 362). The mesquit (*Prosopis juliflora*), which is a tree in the moist river bottoms of the arid Southwest, becomes a sprawling shrub in dry, exposed soil (see also fig. 26). The lower slopes of a mountain in a prairie or desert region often have *Krummholz* which is quite comparable to that toward its summit, and it is made up of species which develop into trees on intermediate slopes, where the rainfall is greater. These and other dwarfed forms of arid soils and climates probably are due to the excessive transpiration in proportion to the limited absorption.

Dwarfing in bogs. — When the bald cypress (*Taxodium*) is grown in upland parks, the trunk is excurrent and the branches symmetrical, but in its natural swamp habitat the main shoot dies after a number of years, and the subsequent vigorous development of lateral shoots results in a spreading crown. Possibly the imperfect absorption which is characteristic of swamps makes it impossible for the water column to rise as high as in other habitats. In western bogs, *Pinus contorta*, elsewhere a slender tree, frequently becomes a gnarled and sprawling shrub, doubtless because of the unfavorable conditions for absorption.

Nanism. — Among the mutants of *Oenothera lamarckiana* there appeared some forms that were much smaller than the parents or the other mutants, and as these dwarfs reproduce true from seed, they were given the specific name, *Oenothera nanella*. Plants of this sort, whose dwarfness appears to be inherent, rather than caused by external conditions, are said to exhibit *nanism*. Similarly, species whose individuals are inherently large are said to exhibit *gigantism*. Experimental cultures have shown that of the many dwarf xerophytes of eastern Sweden, some are inherently dwarf (*obligate dwarfs*), illustrating nanism, while others (*facultative dwarfs*) develop readily into tall plants when grown in favorable conditions. In obligate dwarfs all of the organs commonly are reduced, but in facultative dwarfs the roots and often the flowers are as large as in full-sized individuals; however, experimentation is necessary in order to determine adequately whether any given dwarf is facultative or obligate.

Asymmetric stems. — Most aerial stems tend toward symmetry in their branch development, but asymmetry often is seen, as in trees at the edge of a forest, which branch profusely toward the open, while they are nearly branchless toward the forest interior, probably because of insufficient light. The most striking cases of one-sided trees, however, occur along seacoasts, branch development often being almost entirely inhibited on the seaward side, so that most of the branches point landward. Usually the crown of the tree presents an even slope upward from the seaward side, giving a peculiarly wind-swept aspect, and indicating that the inhibition of branch development is diminished

landward (fig. 363). Two theories have been put forward to account for such asymmetry, neither having adequate experimental evidence; the one maintains that the stronger transpiration on the seaward or windward side causes the branches to die earliest there, while the other theory maintains that salt particles carried in the spray account for branch destruction. It is possible and even probable that both the-

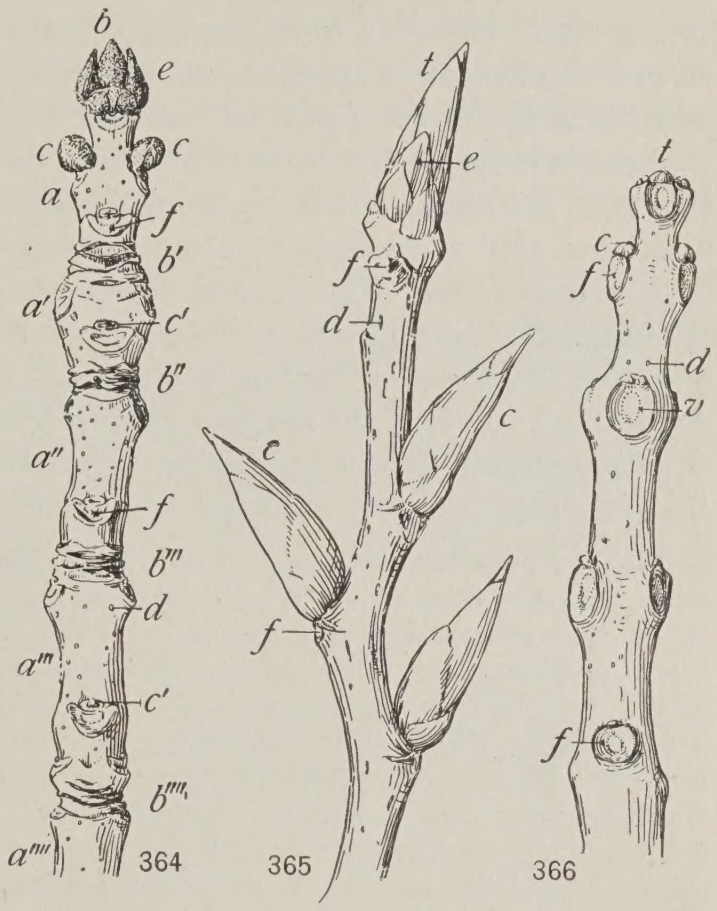
FIG. 363. — Trees of the Douglas spruce (*Pseudotsuga mucronata*) growing near the sea; note the relative absence of branches on the exposed (seaward) side, thus showing the destructive influence of the sea winds; San Juan Island, Wash. — Photograph by O'BRIEN.

ories are valid, the two factors supplementing one another. Apparently favoring the salt theory is the relative absence of one-sided trees about the Great Lakes, but apparently favoring the transpiration theory is the frequent one-sidedness of trees near the " timber line " of mountains.

Periodicity in stem development. — *Periodicity in tree branches.* — The twigs of deciduous trees are made up of alternating dwarfed and elongated portions, the leaf scars of the former being closely grouped, while those of the latter are more widely separated (fig. 364). A

branch begins as a lateral bud closely enveloped by scale leaves, and during the first season growth commonly is slight; the following spring there is a period of elongation accompanied by the fall of the scales, whose position is marked by the closely grouped scars. Later, elongation ceases and there is formed a dwarfed portion, the terminal bud, with closely imbricated scales; in the autumn the leaves fall from the elongated portion, leaving the widely separated scars. Thus the age of a branch may be determined by noting the number either of the dwarfed or of the elongated regions. Sometimes the dwarfed portions are thicker than the elongated portions.

The possible factors. — The factors involved in stem periodicity probably are external, but they have not been determined experimentally. If the terminal bud is removed early in the



FIGS. 364–366. — Twigs, illustrating growth periodicity and the characteristics of winter buds: 364, a twig of an ash (*Fraxinus*), showing alternating regions characterized by slight stem elongation (*viz.* at *b*, the present winter bud; at *b'*, the position of the previous winter bud; at *b''*, the position of the winter bud of two years previous, etc.) and by considerable stem elongation (*viz.* at *a*, representing the growth of the previous summer; at *a'*, representing the growth of the summer previous to that, etc.); note the large size of the terminal bud (*b*) in proportion to that of the lateral buds (*c*); *f*, leaf scar; *d*, lenticels; at *c'* are scars left upon the fall of lateral buds of previous years; 365, a twig of the cottonwood (*Populus deltoides*); note the large buds with imbricated scale leaves (*e*); note also that the lateral buds (*c*) are about as well developed as the terminal bud (*t*); other lettering as in 364; 366, a twig of *Catalpa;* note the small winter buds, both terminal (*t*) and lateral (*c*); note also the prominent circular leaf scars (*f*) with an inner circle (*v*), representing the position of the vascular bundles severed upon leaf fall.

first season, the lateral shoots elongate, indicating that ordinarily the main shoot for a time inhibits elongation in the lateral shoot, possibly because it utilizes the food necessary for the development of the latter (see p. 264). However, when once the lateral shoot begins to develop, its growth phenomena appear to be controlled in the main by definite external factors rather than by an influence residing in the main shoot. Elongation in spring may be associated with the vigorous movement of structural materials at that season, and subsequent dwarfing may be associated with a reduced movement, perhaps supplemented by increased desiccation. The amount of branch elongation varies with the season and is reciprocal to the width of the annual ring (p. 205), maximum elongation occurring in moist and minimum elongation in dry seasons. Differences between twigs of different species (*e.g.* the slender elongated twigs of willows, as compared with the stout twigs of the sumacs) appear inherent rather than related to external factors.

Additional periodic phenomena. — Periodicity is exhibited in the daily growth of stems, elongation being greater by night than by day, as is illustrated by the bamboo, of whose extraordinary growth about two thirds occurs by night. The factors here involved are complex, but may be associated in part with the absence of light (directly or indirectly or both) and with lessened transpiration. Notable periodicity is exhibited by biennial rosette plants (fig. 343), in which, possibly because of insufficient structural material, there is no stem development during the first season, though a vigorous erect stem rises in the second season. Alternating elongated and dwarfed shoots also are illustrated by the summer stems and winter buds of *Utricularia* (p. 194), the phenomena and perhaps the causative factors recalling the situation in tree branches.

Inherent rhythm. — While the plants of uniform climates are evergreen, they are not necessarily continuous growers, though there rarely occurs such definite periodicity as in periodic climates. Some trees, as the coconut and the papaw (*Carica*), are essentially *evergrowers*, developing both vegetative and reproductive organs on the same shoot in unbroken continuity. Probably most trees of the rain forest exhibit what might be termed *spasmodicity* in contrast to periodicity, the varying branches appearing independent of one another and of external conditions; one branch elongates and puts forth new leaves, while another is blooming, another fruiting, and still another is quiescent. When the grape is taken from a temperate region to the rain forest, it develops this spasmodic habit. Such plants, then, are neither uniform evergrowers nor are they uniformly rhythmic, but each branch appears to exhibit a rhythm of its own. It is doubtful, however, if this or any other plant rhythm is entirely unrelated to rhythmic external conditions.

The origin of trees. — The most distinctive features of trees are perennial elongation, perennial diametral increase, perennial lignification, and permanence of tissues. Elongation has been seen to be stimulated

by conditions that favor absorption or impede desiccation, while lignification and diametral increase are favored more by xerophytic conditions. Maximum elongation, on the whole, occurs in the tropical rain forest, where trees are predominantly tall and slender, though the tallest individual forms, *Sequoia* and *Eucalyptus*, occur in much drier regions. Maximum diametral increase occurs, on the whole, in relatively arid climates. It is sometimes stated that the baobab, a xerophytic African tree, has the greatest diametral growth of all known

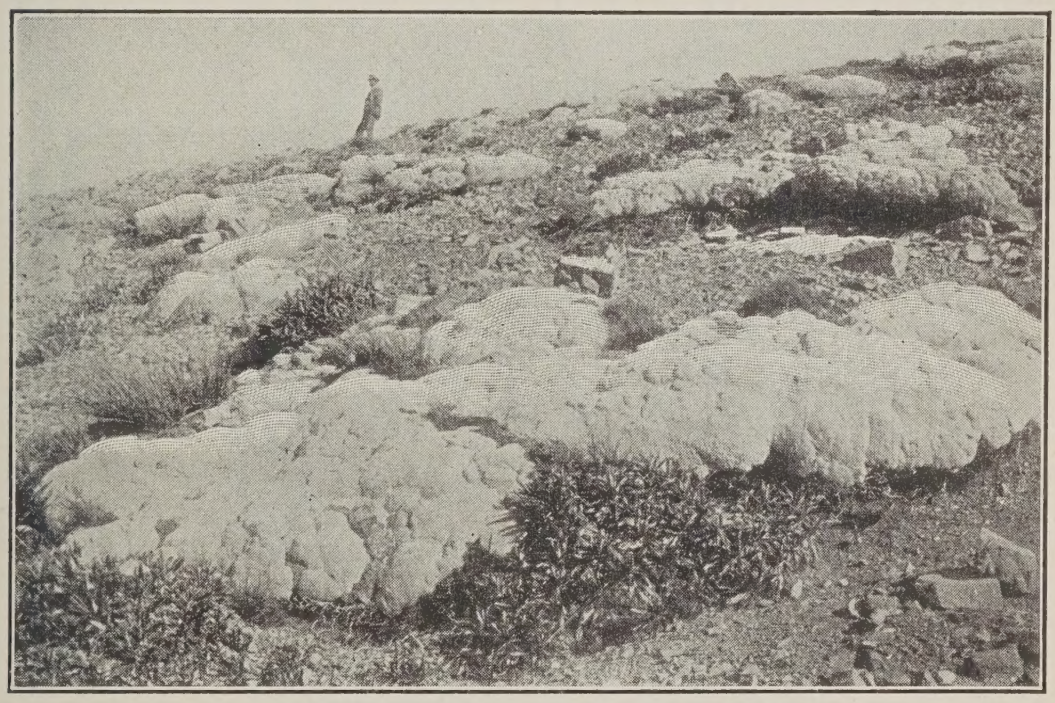
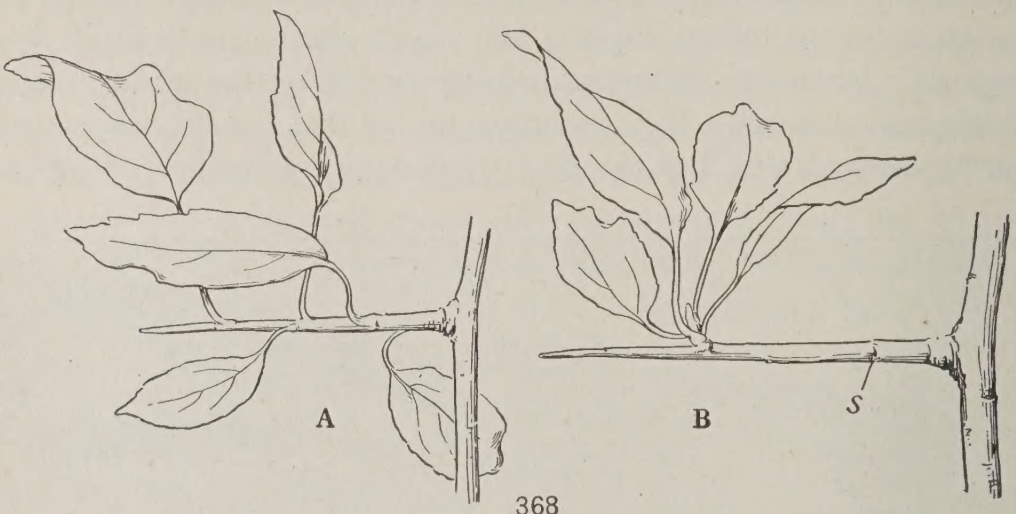


FIG. 367. — The mountain sheep (*Raoulia eximia*), a remarkable alpine composite, illustrating the culmination of the cushion habit among seed plants; each coral-like colony is composed of thousands of separate but closely compacted shoots, the whole mass being attached to solid rock by a single root system; New Zealand. — From COCKAYNE.

trees; other xerophytic trees with great diametral enlargement are the dragon tree (*Dracaena draco*) and *Cavanillesia*. However, some trees of great diameter (as the redwood and the hemlock) are mesophytic.

Doubtless the tree habit has originated many times and in many habitats. Sometimes it has been assumed that the tree habit is a result of the "struggle for existence" in mesophytic climates; this, perhaps, is a tenable view, since growth in dense cultures increases stem elongation. However, there is equal reason for believing that trees have arisen also in dry regions, since lignification and diametral

enlargement are best developed there. Perhaps the most essential step in the evolution of the tree habit is in the passage from an herb to a shrub; if so, experiments on such plants as *Spiraea latifolia* and



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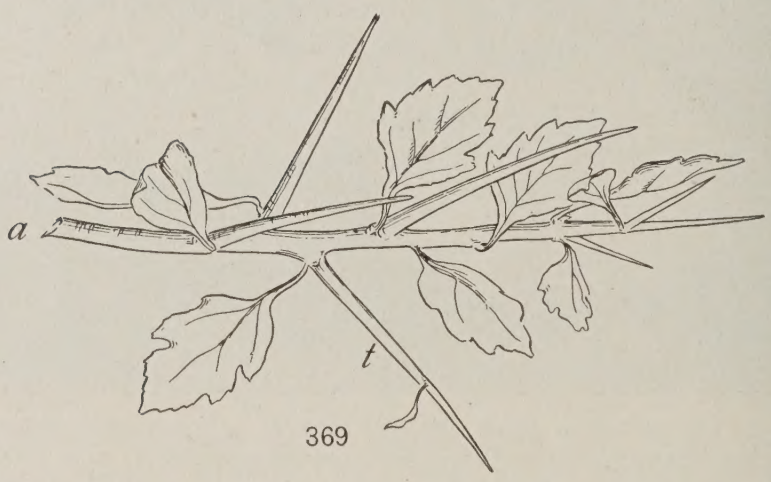

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FIGS. 368, 369. — Spinose branches: 368 A, a spinose branch of the wild crab apple (*Pyrus coronaria*) in its first year; note that the terminal bud soon ceased to develop; 368 B, a similar branch in its second year, showing a lateral bud that continued to develop; *s*, leaf scar indicating the position of a leaf of the first season; 369, a compound spinose branch of a hawthorn (*Crataegus punctata*), showing that such spines are branches whose terminal buds soon cease development; note that leaves occur on the lateral branches (*t*), as well as on the main axis (*a*).

Amorpha canescens, which are sometimes one and sometimes the other, might throw light upon the problem.

The advantages of variation in stem form. — The capacity for differential elongation possessed by aquatic stems and by many aerial stems when submerged by sand is of obvious advantage in that the lifting of the leaves into the light and the air is thus made possible. Of

unusual significance is stem dwarfness, as illustrated by cushion plants and by the *Krummholz*, since such habits are admirably suited for protection, especially from excessive transpiration. Such protection is due in large part to the reduced surface exposure resulting from the compact arrangement of the parts. For example, in *Raoulia* (fig. 367) and in other alpine or arctic cushion plants, the short stems are so closely packed together that only the tips are exposed. Cushions are

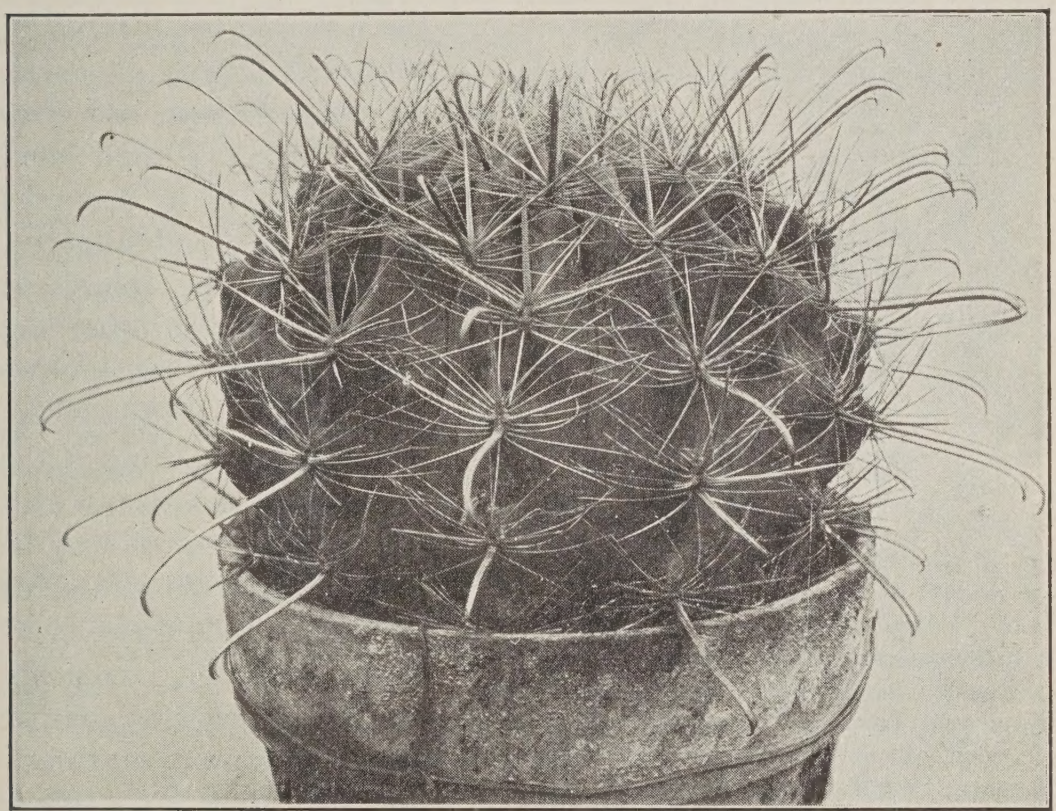


FIG. 370. — A spherical cactus (*Echinocactus wislizeni*), representing an extreme contrast to a thin-leaved tropical evergreen, since it has a minimum transpiring surface in proportion to its volume; note the numerous recurved spines. — Photograph by FULLER.

formed by various mosses (as *Leucobryum*, *Bartramia*, and *Dicranum*) and by some lichens (as *Cladonia rangiferina*, fig. 204), but among seed plants the habit is rare outside of inclement climates. An additional advantage from dwarfness is increased ground protection; as a consequence, transpiration is still further reduced and temperature changes are less rapid. Perhaps the advantages of proximity to the ground are best realized in rosette herbs, whose leaves often are closely appressed to the soil (fig. 343). A third and perhaps the greatest advantage in dwarfness is seen where the latter is most in evidence, namely,

in alpine and arctic regions. There it makes possible protection by snow, and consequently there is a suspension of transpiration during the very months when it would be most dangerous because of the cessation of absorption; furthermore, snow covers protect greatly from cold. So severe are the conditions at times that only those parts covered by the snow are able to survive.

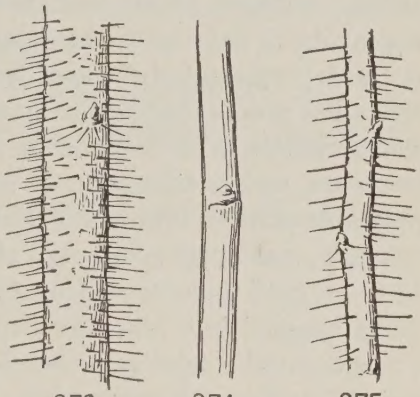
Spinescence. — *The structural features of spines.* — Stem spines are of two fundamentally different sorts, namely, reduced branches, as in the honey-locust (*Gleditsia*), wild crab (*Pyrus coronaria*, fig. 368), *Prunus*, and *Crataegus* (fig. 369), and stem emergences, as in the roses (figs. 373, 375) and the gooseberries. In the spinescent branches, which often are compound, the branch character usually is easily recognized in youth through the presence of leaves and axillary buds, and scars may be found even on old spinescent branches. Spinescent emergences, however, commonly are simple, and may be either stout thorns or delicate prickles; both kinds occur in the roses, the former near the leaves, and the latter scattered along the stem. Perhaps the culmination of spinescence is seen in cacti (figs. 370, 347–349), where all gradations occur between the stoutest thorns and the most delicate prickles.

FIGS. 371, 372. — Spinescence in *Ulex europaeus*: 371, an individual grown in saturated air; note the conspicuous leaves; 372, an individual grown in dry air; note that the branches are reduced to spines. — From LOTHELIER.

The factors determining spinescent branches. — Experiments on *Ulex*, *Berberis* (figs. 191, 192), and other plants show that spinescence may be induced by intense light and especially by desiccation; in *Ulex* the shoots developed in moist air bear foliage leaves, while in dry air the branches and even the leaves become spinescent (figs. 371, 372). *Pyrus coronaria* and *Prunus americana* are much thornier in xerophytic than in mesophytic situations; *Celtis occidentalis* (the hackberry) is a spineless mesophytic tree, while *Celtis occidentalis*

pumila is a thorny xerophytic shrub. Thus such spinescence seems to be a result of hard conditions, the branches remaining reduced because of pronounced desiccation, supplemented, perhaps, by other factors. Individuals of *Ulex* grown in concentrated glucose solutions develop spines even in moist air. It has been claimed that the leafy shoots of *Ulex* usually developed in moist air are merely juvenile shoots.

Spinescent branches, as appears from the preceding, are dwarfed shoots, and are produced much as are other dwarfed stems. However, there is no tendency toward lateral enlargement, as in most dwarfed stems, but rather the reverse, since one of the chief characteristics of spines is attenuation. If elongation occurs when the growth conditions are very favorable, and lateral enlargement accompanied by dwarfing when they are less favorable, then attenuation with dwarfing (*i.e.* spinescence) may be a result of very unfavorable conditions. Attenuation seems to imply progressive severity in the developmental conditions, the supply of structural material becoming less and less as the branch develops. Furthermore, there is an increasing development of mechanical tissue in proportion to the other tissues, the tip being composed chiefly of thick-walled elements, which account for its extreme stiffness; this fact also fits in with the desiccation theory of spinescence. Desiccation does not account readily for all spinescent branches, since *Crataegus* and *Gleditsia* develop them profusely in moist and fertile flood plains; furthermore thorny lianas are extremely abundant in humid tropical forests.



FIGS. 373–375. — Variation in prickle development on the stem of a wild rose (*Rosa blanda*): 373, a portion of a young root sucker of a mesophytic individual; note the abundance of prickles; 374, a portion of a branch from the same stem, showing an entire absence of prickles; 375, a portion of a branch from a xerophytic individual, corresponding to that figured in 374; note the numerous prickles.

The factors determining spinescent emergences. — The cause of spinescent emergences is much more difficult to determine than that of spinescent branches. Their variation is considerably less and their development is not so obviously related to severe conditions. The stem of *Rosa blanda* frequently is smooth, but in xerophytic conditions, prickles appear in abundance (figs. 373–375); oddly enough, abundant prickles also characterize vigorous rose and gooseberry suckers in mesophytic habitats. So far as desiccation or other hard conditions favor the development of spinescent emergences, as in the roses, there might seem to be agreement with *Ulex*, but there is the fundamental

difference that here desiccation causes the appearance of a new organ rather than the reduction of an organ commonly better developed; in other words, the influence of an increased supply of water is directly inhibitory. Thus desiccation in the case of prickles and of other spiny emergences, much as with the hairs of *Polygonum amphibium* (p. 90), has a determinative rather than a formative influence, as in the case of spinescent branches. Possibly many spines and prickles are obligate rather than facultative.

Spines and "natural selection." — A curious though widely accepted view is that spines have been evolved by "natural selection" through age-long "competition" between plants and grazing animals. It has been supposed that plants happening to have spines have survived and had progeny, while many others without such "weapons of defense" have failed. While the xerophytic theory of spinescence has good experimental proof, the selection hypothesis has almost none, the sole argument in its favor being derived from overgrazed pastures, where thistles, brambles, and hawthorns tend sometimes to increase their area in place of more palatable plants. Many considerations weaken the force of this argument. For example, spinescent plants are not necessarily unpalatable; hawthorns are eaten by cows, until they can no longer reach the foliage, the lower parts of the trees often being cropped into fantastic shapes; it is reported also that in Arizona grazing animals avoid a relatively thornless cactus (probably because of its flavor), while greedily eating a thorny variety. Furthermore, most thorns are tender and more or less edible when young, that is, when the plants most need protection.

As a whole, the plants most eaten by grazing animals are grasses, and it is well known that grasses flourish as a result of grazing; indeed, one of the prominent theories attempting to account for the prairie is that grazing animals keep down shrubs and trees. Grasses increase and trees decrease in pastures in the Central States, because the former have underground propagative organs and the latter not, spinescence being a negligible factor. In the Eastern States shrubs and trees, whether spinescent or not, rapidly invade pastures because of the favorable climate, in spite of the combined influence of rhizomatous herbs, farmers, and grazing animals. However, there are still stronger arguments against the selection theory. In the first place, the close confinement of grazing animals is a recent and insignificant thing in biological history; the overplus of vegetation always has been so enormous that the influence of herbivorous animals on plant evolution must have been infinitesimal. In the second place, the culmination of spinescence is in deserts, where grazing animals are scarce, and where "competition," if such exists, is least important. Finally, in so far as "natural selection" is applicable to the problem of spinescence, its influence has to do with the survival of spinescent plants rather than with the origin of their spines.

The advantages of spines. — Probably spines and prickles are of some advantage as a means of protection from herbivorous animals, though this advantage has been greatly overestimated. The perpetuation of

thistles in sheep pastures doubtless is due in part to leaf spinescence, and the thorniest cacti (fig. 370) certainly are amply protected from the incursions of ordinary grazing animals. In the holly the upper leaves, which are out of the reach of grazing animals, are less spinescent than are the lower leaves. In the cacti, spines often are abundant enough to lessen the intensity of the incident light, thus, perhaps, reducing transpiration. Thorns are of undoubted advantage in the climbing of many lianas (p. 171). Probably many and perhaps most spines subserve no rôle of importance; in *Gleditsia* they occur chiefly on old and inedible branches, while the tender young shoots commonly are spineless; the increased spinescence of xerophytic forms (as in *Ulex* and *Rosa*) appears to have no advantage.

Tuberization. — *Early experiments.* — Tubers represent the culmination of stem shortening accompanied by diametral enlargement

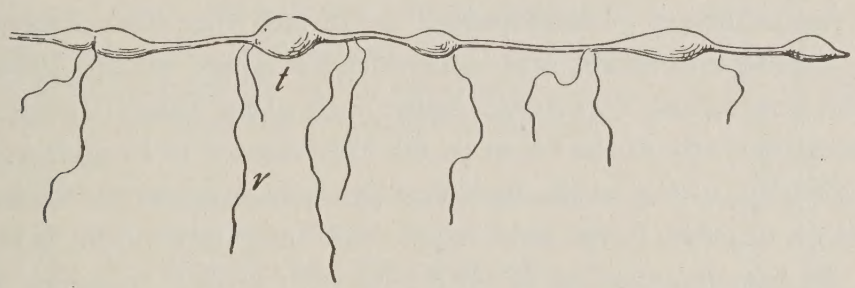


FIG. 376. — A rhizome of *Scutellaria parvula*, in which there has taken place alternately stem elongation and tuberization; *r*, adventitious roots; *t*, tuberized portions.

(figs. 376, 291, 297, 298), and commonly they accumulate quantities of food and water which are utilized when their buds develop into shoots. Experiments show that tuberization is directly favored by darkness and checked by light, although indirectly light favors tuberization in that it stimulates food formation in the foliage leaves. The removal of all rhizomes from a developing potato plant results in tuber formation on aerial shoots, regardless of illumination. Moderate desiccation favors tuberization, while moisture often inhibits tuber formation (as in the potato and in species of *Juncus*). Low temperatures appear to favor tuberization, only tuber-bearing shoots developing in the Marjolin potato below 7° C., while only leafy shoots develop above 20° C.; horizontal tuber-bearing shoots may be transformed into erect leafy shoots by raising the temperature, and the reverse transformation may be effected by lowering the temperature. More heat is necessary to transform dextrose into cellulose than into starch; this may explain the abundant formation of starch accompanying tuberiza-

tion at relatively low temperatures, and the great formation of cellulose associated with elongation at high temperatures. There appears to be a reciprocal relation between leafy shoots and tuberized shoots, any factor tending to suppress the former stimulating the development of the latter; for example, tuberization is induced by various substances which check the growth of shoots. An instance of tuberized aerial stems is seen in the kohl-rabi; even the leaves of this plant become tuberized if flowering is suppressed. Similar tuberous swellings occur on the stems of *Eucalyptus;* neither in the kohl-rabi nor in *Eucalyptus* are the stimulating factors known except that in the former, light is necessary, and that in the latter, the size increases with the food supply. In *Nephrolepis* similar primordia may, as the conditions vary, give rise to rhizomes, runners, or tubers.

The fungal theory of tuberization. — It has long been known that tubers almost universally are infected with fungi, potato tubers, for example, containing *Fusarium solani* and other fungal forms. The experimental study of the tuber problem as related to fungi is attended with difficulty, owing to the fact that the isolation and the subsequent cultivation of tuber fungi, as of mycorhiza fungi in general, is far from easy. As yet, inoculation experiments with potato rhizomes are uncertain in their results, but in many orchids, where fungal symbiosis is more obligate than elsewhere, some exceedingly suggestive studies have been made. As a class, orchids have two growth periods, one of relatively active differentiation and elongation, and another of lessened activity and diametral increase, that is, of tuber formation. Tuberization may involve the roots, as in *Habenaria,* the underground stem, as in *Aplectrum,* or the aerial stem, as in most epiphytic forms. It has been shown by inoculation experiments and otherwise that tuberization is initiated when the stem or root is infected with the proper fungus, the latter organism appearing to arrest the growth of the terminal bud and to cause the development of hypertrophied cells. Shoots arising from infected tubers are at first free from fungi, and they differentiate rapidly until they in turn are infected, whereupon tuberization sets in, so that usually there is one period of infection and tuberization each year in a given rhizome or root. In the shoots of *Neottia,* however, fungal infection and tuberization are present from the start. Simultaneously with tuberization starch accumulation is greatly accelerated.

Circumstantial evidence favoring the fungus theory. — When the potato was first introduced into France, gardens sown to tubers produced crops of tubers, while gardens sown to seed produced no tubers, the inference being that the fungi from the old tubers infected the new tubers, whereas the seeds were free from fungi. Nowadays seed cultures produce crops of tubers, presumably because the soil has by this time become infected with the necessary fungus. The gametophytes of *Lycopodium* and *Botrychium* are tuberous and are infected by fungi when subterranean, but not when aerial (fig. 377). The root tubercles of legumes (see p. 303), which are known to be the direct result of bacterial infection, resemble tubers not alone in the replacement of elongation by lateral enlargement, but also in the great accumulation of food and water in the hypertrophied cells. Again, in many fungus and insect galls (as in the cedar apple and in cynipid oak galls), elongation is checked, while diametral increase and the accumulation of food and water are greatly stimulated; the food may accumulate even in definite carbohydrate and protein layers. Thus root tubercles, galls, and tubers agree in all essential structural features; root tubercles and galls admittedly are due to the influence of outside organisms, and it seems fairly certain that the same is true of tubers.

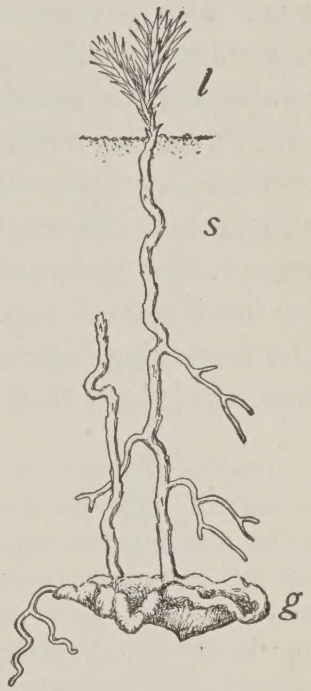


FIG. 377. — The subterranean tuberous gametophyte (*g*) of *Lycopodium annotinum*, bearing a young sporophyte (*s*), whose aerial portion has numerous awl-shaped foliage leaves (*l*) in many orthostichies. — From BRUCHMANN.

If a gall is defined as a structural modification due to a foreign organism, then potato tubers and the gametophytes of *Lycopodium* and *Botrychium* may be classed as galls, if the fungus theory is confirmed. The fact that tubers and root tubercles are advantageous, as is not true of many fungus galls and of most insect galls, is of no significance from the standpoint of causation, and would seem unimportant in classification; the harmful root tubercles caused by nematode worms and the beneficial root tubercles caused by bacteria are remarkably alike in form and origin, and may well be classed as similar structures.

Bulbs, as well as tubers, commonly are infected with fungi, which, therefore, may have formative significance, though the case is much more doubtful than with tubers. While bulbs agree with tubers in possessing shortened stems, they differ in that lateral stem enlargement is replaced by hypertrophied growth and by food accumulation in the scale leaves. *Arrhenatherum bulbosum* has been shown to be merely a bulbous form of *A. elatius*, resulting from bacterial infection.

The nature of the fungal influence. — In orchids and in the potato, tuberization has been induced in concentrated solutions (as of saccharose or glycerin) without the agency of fungi; similarly in the onion, bulb formation has been induced in sterilized cultures. When

radishes are grown in concentrated glucose solutions, the root becomes suberized, somewhat resembling a potato tuber, and starch accumulates instead of sugar. Apparently, then, tuberization may result when the osmotic pressure in the culture medium is high, though this does not appear to be the sole factor, since solutions of glucose and glycerin of equal pressure give different results. Certainly for starch formation, and perhaps for tuberization, the presence of abundant sugar also is necessary. Since fungi commonly have a much more concentrated cell sap than do other plants (p. 270), it seems very probable that the rôle of fungi in tuberization is in raising the concentration of the media which they enter; indeed, it has been demonstrated that *Fusarium* cultures in macerated preparations of potato tubers raise the concentration. Very probably tuberization resulting from low temperatures or from soil dryness may be similarly explained by increased cell sap concentration. In some cases (as in the radish) the increasing concentration of the sugar manufactured by the leaves may alone be sufficient to stimulate tuberization.

Stem succulence. — As in leaves, so in stems, succulence appears to be of two fundamentally different sorts, namely, halophytic and similar succulence, in which water accumulation appears to be associated with a concentrated cell sap, and the sort of succulence found in the cacti, which rarely occur in alkaline situations and whose cell sap is not known to be particularly concentrated. In *Salicornia* and in other fleshy halophytes, succulence has been shown to vary with the salt content of the medium, and the retention of water would appear to be due largely to the presence of salts. In the cacti and in similar forms the retention of water probably is due in large part to a thick cuticle and to other relatively impermeable tissues, supplemented by a small transpiring surface. As stated elsewhere (p. 146), the cells of succulent plants do not necessarily contain more water than do those of other plants, but they are more compactly placed. Axial shortening and diametral enlargement are significant features of succulent stems, and in these respects such stems agree with tubers and with xerophytic stems generally; furthermore, these features appear to be due to similar causes.

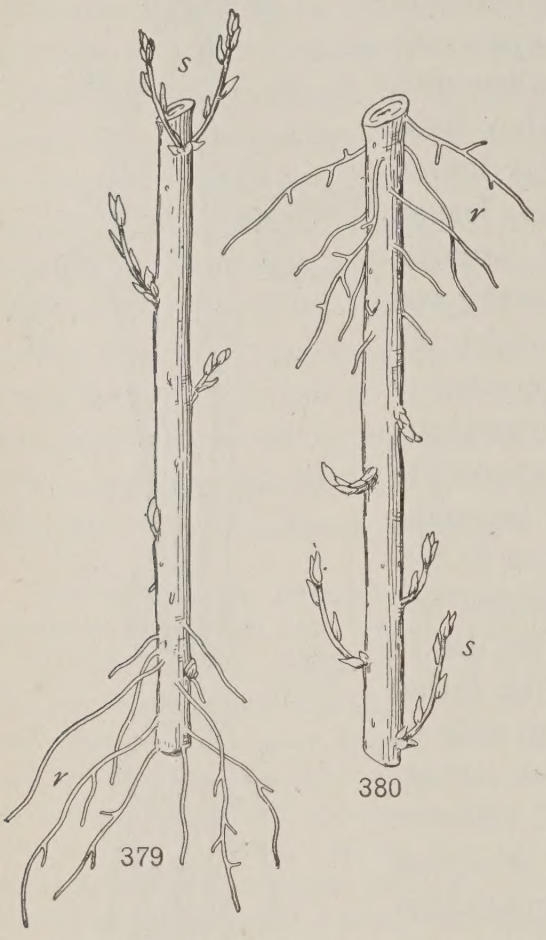
Correlation; regeneration; polarity. — *Correlation.* — In the preceding chapters much has been said concerning the influence of explicit external factors, such as light, temperature, and water; allusion has been made also to internal or inherent factors, which are supposed to represent hereditary as opposed to environmental influences. Intermediate between these are influences residing within the organism, but not hereditary, such as the influence of one cell or organ upon the development of another. Phenomena due to such influences are

known as *correlations*. If an individual of *Sempervivum assimile*, ordinarily a stemless plant with succulent leaves, is removed from its natural dry habitat to a moist chamber, there soon develops as a reaction to the new conditions an erect stem, on which the first leaves also are succulent (figs. 350, 351). After a time thin leaves develop, whereupon the stem ceases to elongate. Here axial elongation is correlated with thick leaves, and axial shortening with thin leaves. Many plants (as *Penthorum* and *Satureja*, figs. 290, 293) possess erect or *orthotropic* and horizontal or *plagiotropic* shoots, which obviously are correlated, since the removal of the former causes the latter to become erect; the presence of the erect shoot appears to inhibit the horizontal shoot from becoming erect. The reference of phenomena to correlation, or for that matter to inherent factors, does not explain them. The use of such indefinite terms is mystifying rather than illuminating, and explanations must be sought in actual underlying causes. However, terms like correlation and inherent causes may be useful temporarily, as serving to denominate these particular regions of our ignorance.

FIG. 378. — Regeneration in the scarlet runner bean (*Phaseolus multiflorus*) the epicotyl of a seedling was cut away, whereupon the minute primordia in the axils of the cotyledons developed into vigorous shoots. — After MCCALLUM (drawn from a photographic reproduction).

Regeneration. — In most plants the terminal buds are stronger than the others, and they develop into vigorous shoots (figs. 260, 261); the upper lateral buds develop into less vigorous shoots, and the lower lateral buds usually remain undeveloped. Such plants are characterized by excurrent branching. In some cases (as in the lilac) the lateral buds are the stronger, and their continued development results in deliquescent branching. If a terminal bud of an excurrent shoot is injured or removed during development, one or more lateral buds, which otherwise might have

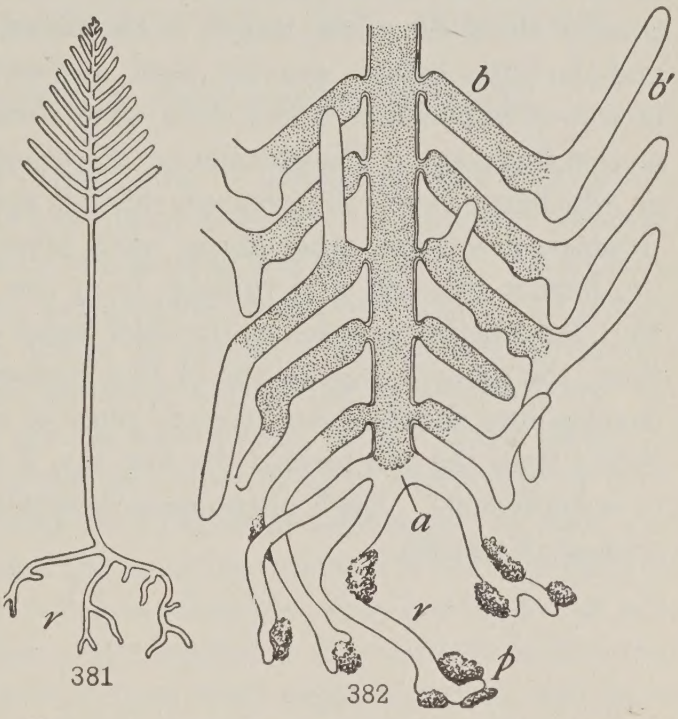
remained latent, grow out into shoots (figs. 179, 362). Such a replacement by similar organs of an organ that has been removed, or whose growth has been checked, is known as *regeneration*. In animals a lost part commonly is regenerated at the place of severance. This rarely occurs in plants, possibly because of the presence of latent buds. In roots and in some leaves (as in *Cyclamen*), where there are no such latent buds, the lost part may be restored at the cut surface, as in animals (p. 19); the regeneration of a lost part at the cut surface may be termed *restitution*.



FIGS. 379, 380. — Polarity in a willow (*Salix*): 379, an ordinary erect cutting; 380, a cutting that has been grown in an inverted position; note that in each case the roots (*r*) arise from the basal portion of the stem (root pole) and the new shoots (*s*) from the apical portion of the stem (shoot pole). — After PFEFFER.

When a growing tip is removed, the latent buds that develop and replace it commonly are those nearest the apex. If these are removed, those next below develop, and so on until no more buds remain. A remarkable instance of this is seen in *Phaseolus* (fig. 378), where buds in the axils of the cotyledons may thus be induced to develop into shoots. If all buds are removed, new buds may organize, as from the exposed part of the cambium ring in a beech stump. The factors operative in regeneration are unknown, the current theory relating the phenomena to correlation; for example, a main shoot is supposed to inhibit the development of lateral shoots, possibly because it utilizes the available food through having a better position or through making an earlier start. The suppression of the main shoot removes the inhibition, and permits the lateral shoots to develop. Such a conception is of value chiefly in stating the problem.

Polarity. — If a willow shoot is placed in water, shoots develop from the uppermost buds, and roots originate near the base. If the shoot is inverted, roots develop above and shoots below (figs. 379, 380). Such a phenomenon illustrates *polarity*, and appears to indicate that plants and portions of plants possess root poles and shoot poles. Among other instances of polarity, there may be cited the appearance of shoots at the uppermost parts of exposed roots of *Crataegus* (fig. 23), of buds at the basal portions of severed leaves in *Sansevieria* (fig. 240), and of tubers on the upper ends of reversed shoots of the potato.



FIGS. 381, 382. — Reversal of polarity in an alga, *Bryopsis muscosa:* 381, an ordinary plant (somewhat schematic); 382, the apex of a plant that has been grown in an inverted position; note that rhizoids (*r*) have developed from the apex of the shoot (*a*), and that shoot branches (*b*) nearer the original rhizoid pole have continued to develop as branches but have taken a new direction (*b'*); the dotted portions represent the original part of the plant before inversion, while the undotted portions represent portions growing after inversion; note the intimate contact between the rhizoids and the soil particles (*p*); this alga is a coenocyte, being from the outset without internal cell walls; considerably magnified. — After NOLL.

Attempts have been made to explain polarity by postulating the existence in plants of *shoot-forming substances* that migrate upwards and of *root-forming substances* that migrate downwards. In a willow branch new shoots develop toward the apex, where the shoot-forming substances are supposed to congregate in greatest abundance, and new roots develop toward the base, where the root-forming substances are thought to be most abundant. Apparently favoring this theory is the fact that severed old leaves of *Begonia* or of *Achimenes* regenerate shoots that soon produce flowers, whereas shoots developing from young leaves do not develop flowers for some time, as though old leaves were much fuller of *flower-forming substances*

than are young leaves. However, until something is known concerning these postulated substances, the theory must be regarded as mystical if not actually erroneous.

To some extent tendencies toward polarity may be counterbalanced by external factors; for example, if a willow shoot is laid horizontally in the water or on the soil, shoots and roots often develop more or less equally along the whole length of the shoot, the former chiefly above and the latter below; gravity, light, and water probably enter here as factors of importance. In *Zamia*, shoots may appear at both ends of a stem fragment. The gemmae of *Marchantia* develop chlorenchyma on whichever side is illuminated, rhizoids appearing on the other side. *Bryopsis* and some other algae, when reversed, develop shoots from the former rhizoids, and rhizoids from the former shoots (figs. 381, 382), light being regarded as the chief factor determining shoot formation; the roots of *Neottia* and of *Platycerium* under similar conditions develop into shoots. An inverted piece of a dandelion root develops shoots from the end toward the root tip, if the other end is in water or is kept moist. Such phenomena illustrate what has been termed a *reversal of polarity*.

CHAPTER IV — SAPROPHYTISM AND SYMBIOSIS

1. COMMENSALISM AND SAPROPHYTISM

Symbiosis and related phenomena. — *Autophytes* and *heterophytes.* — The preceding sections have been devoted to a detailed consideration of the ecological aspects of nutrition in green plants. Such plants may be termed *autophytes*, autotrophic plants, or independent plants, because they are able to obtain all necessary food materials directly from inorganic sources, subsequently converting them into foods. In striking contrast thereto are the *heterophytes*, heterotrophic plants, or dependent plants, whose existence depends upon antecedent or coexistent organic forms, because they derive at least a part of their food from organic sources. Since the nutritive relations of the heterophytes are so different from those of the autophytes, they are made the subject of a separate chapter. Heterophytes may be subdivided into *saprophytes*, which obtain food from dead organic matter, and *parasites*, which obtain food or food materials from living organisms.

Symbiosis. — When two or more diverse organisms live together in more or less intimate relationship, the phenomenon is termed *symbiosis*, and the individual organisms are termed *symbionts*. The phenomena included in symbiosis may be conveniently grouped into *disjunctive* and *conjunctive symbiosis* and each of these groups separated into *social* and *nutritive* subdivisions. In *social symbiosis* is included all cases of dissimilar organisms living together without any direct organic connection or food relationship and it may be applied to the relations existing between the organisms in a plant community. In *nutritive symbiosis*, on the other hand, one or more of the symbionts derives food directly from the other symbiont. This food relationship may be one of *antagonistic nutritive symbiosis*, or *parasitism*, in which one organism, the *parasite*, derives food or food materials from another, the *host*, to the detriment of the latter. Sometimes each symbiont derives food from the other (as in the case of clover and bacteria) a relationship that may be termed *reciprocal nutritive symbiosis* or *re-*

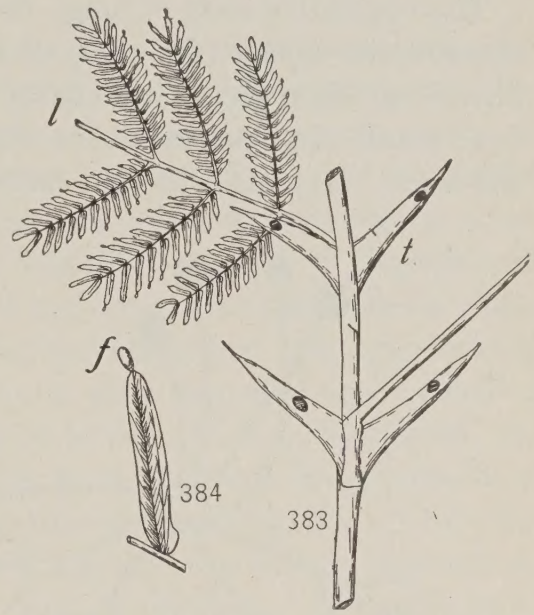
ciprocal parasitism. *Commensalism* includes those cases of symbiosis in which two or more organisms live together with possible benefit to some or all of the symbionts, but with injury to none. The individuals in commensalistic symbiosis are termed *commensals*. Dependent and interrelated plants thus may be divided into three classes: commensals, which are symbiotic but not necessarily heterotrophic; saprophytes, which are heterotrophic but not symbiotic; and parasites, which are both symbiotic and heterotrophic.

Commensalism. — *Commensalism between plants.* — The liverworts, *Anthoceros* and *Blasia*, and the water fern, *Azolla*, contain colonies of the alga, *Nostoc*, in certain rather definite regions of the plant body; it is not known that either of the commensals derives any particular benefit from the association, though it may be supposed that the alga has a somewhat better protected and more uniformly moist habitat than when it lives independently. Palmetto trees are inhabited by certain characteristic epiphytes, probably because the soft bark provides an easy place for them to become established; similarly certain trees have characteristic lichens that doubtless are associated with some physical or chemical peculiarities of the bark. Such associations may be regarded as illustrating a sort of loose commensalism, and the same may be said of the characteristic associations of microörganisms which live in the slimy coats of water lily leaves. The relationship of a liana to its support is still less intimate, since one tree serves as well as another. There exists an easy transition from such a loose commensalism as that of the water lily leaf to a representative plant association like a forest, where the shade benefits the mosses underneath the trees, and where the moisture conserved by the mosses benefits the trees.

Myrmecophytes. — The best examples of commensalism are found among animals or in such associations of plants and animals as those between plants and ants. In the tropics, many ants establish *domatia* (*i.e.* abodes) in the internal cavities which occur in various plants; in *Cecropia* the domatia consist of large chambers, and in *Myrmecodia* they consist of chambers connected by labyrinthine passages. In *Acacia sphaerocephala*, hollow thorns serve as domatia (fig. 383), and albuminous food bodies at the ends of the leaf pinnules are eaten by the ants (fig. 384); in other plants nectar secretions are utilized similarly. Such plants are known as *myrmecophytes* (*i.e.* ant plants). The ants that live in myrmecophytes have been said to be very warlike and to defend their domatia with great vigor; such commensalism has been regarded as mutualistic, the plants which serve as an abode and as a source of food for these ants, supposedly being protected by them from leaf-cutting ants. Certain studies afford this theory little support, demonstrating that the interrelation is comparatively incidental and that the plants gain little or nothing from

the symbiosis; leaf-cutting ants are not so destructive as has been supposed, and they are absent in many regions where myrmecophytes are abundant (as in Malaysia); furthermore, the commensalistic ants (as *Azteca*) usually are without effective weapons of offense and are not disposed to attack intruders. The domatial chambers develop quite independently of ant stimulation.

A remarkable case of symbiosis is found among certain South American leaf-cutting ants. The fungus, *Rozites gongylophora*, is said to furnish the sole food of certain ants, which cultivate it in their "fungus gardens." The ants cut off leaves and take them to the "gardens," where they serve as food for the fungi. Similarly, the termites or white ants have "fungus gardens," and even are supposed to weed out undesirable fungi.



FIGS. 383, 384. — A myrmecophyte, *Acacia sphaerocephala:* 383, a portion of a shoot, showing part of a doubly pinnate leaf (*l*), whose pinnae terminate in "food-bodies"; note the hollow paired thorns (*t*) which are punctured by ants that live within the thorns; 384, a single pinna with its terminal "food-body" (*f*), somewhat enlarged.

Saprophytism. — *General considerations.* — Saprophytes are defined as plants that obtain their food from dead organic matter, appearing to contrast sharply on the one hand with autophytes or independent plants, and on the other hand with parasites, which derive their food from living organisms. However, careful study has shown that all gradations occur between saprophytes and autophytes and between saprophytes and parasites, making it often a matter of extreme difficulty to determine how certain plants should be classified; indeed, in many cases a particular plant may vary in its nutritive relations, belonging sometimes to one group and sometimes to another. Those plants which obtain all their food from dead organic matter may be termed *holosaprophytes*, while those plants that are partially saprophytic and partially autophytic may be termed *partial saprophytes*. The more facultative or plastic forms, which may live as autophytes, as saprophytes, or as partial saprophytes, may be termed *mixophytes*.

Saprophytism in the fungi and bacteria. — The most representative holosaprophytes occur among the fungi and bacteria. Among the common saprophytic bacteria are the nitrifying organisms of soil and

water, the organisms causing the putrefaction of meat and the decomposition of milk, and the bacteria of hay infusions. Among the commoner saprophytic fungi are the molds (*e.g. Penicillium* and *Mucor*, fig. 385), the yeasts, and most fleshy fungi. Saprophytic fungi and bacteria occur wherever there is dead organic matter, particularly in humus, the processes of decay being associated with these organisms.

The vegetative body of fungi, the *mycelium*, is composed of delicate threads, the *hyphae* (fig. 385), which penetrate the substratum in all directions, often giving it a characteristic color, as in white or yellow dead wood. In *Lycoperdon*, the hyphae form rootlike strands of different sizes. Hyphae, like root hairs, are filamentous plasmatic struc-

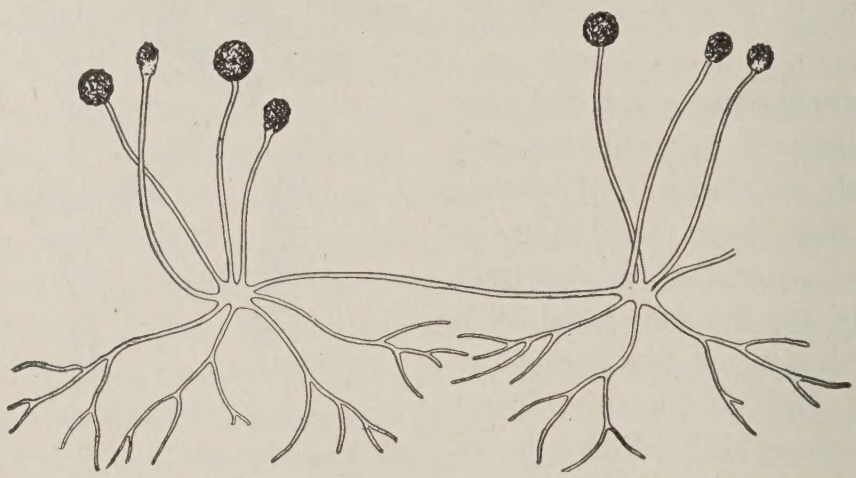


FIG. 385. — A diagrammatic representation of a common mold (*Mucor*), showing branching rhizoid-like hyphae which get food from the substratum; note also the globular sporangia borne on stalks, the sporophores; considerably magnified. — From COULTER.

tures with permeable thin walls, but as might be expected from their heterotrophic relations, they appear to surpass root hairs as organs of absorption, probably because of their greater power of penetration and because of the higher concentration of their cell sap. Some hyphae penetrate dead bark and wood mechanically, chiefly through cracks and wounds, while others secrete enzymes, which increase the solubility and digestibility of many of the materials in the substratum. Fungi secrete organic acids much more actively than do root hairs, and thus are more potent factors in disintegration. But it is probably the concentrated cell sap that is chiefly responsible for the absorptive efficiency of fungi, since this makes possible not only a wider range of habitats (as jelly and sirup, in which root hairs cannot develop), but also the absorption of a greater number of substances such as various organic compounds (qualitative efficiency), and the greater absorption

of various substances, such as water (quantitative efficiency). Perhaps another advantageous feature in hyphae is the fact that cross walls are absent for long distances. Thus it seems very probable that hyphae flourish much better than do root hairs, when the two develop in a common medium, such as the forest humus; this appears to be a consideration of great importance in connection with the mycorhiza plants.

Saprophytism in the algae. — Algae as a class possess synthetic pigments and are autophytic, these being the chief characters that distinguish them from fungi; however, the saprophytic potentiality of many algal forms has been established. Some plants that are classed as algae are habitually saprophytic and colorless, particularly some of the Peridineae and diatoms (as *Nitzschia putrida*); in *Euglena* and in various diatoms, the members of a given species sometimes are pigmented and presumably autophytic, and sometimes they are colorless and presumably saprophytic. In one alga, supposed to be *Carteria* or a closely allied form, there appears to be nutritive dimorphism, approximately half of the individuals in each colony being pigmented and autophytic, while half are colorless and saprophytic. A cave-inhabiting form of *Gloeothece rupestris*, namely, the variety *cavernarum*, habitually utilizes organic food and is colorless. Comprehensive experiments show that many species of the lower algae may flourish in darkness, even when organic acids (as acetic acid) are the only source of carbon. If organic substances occur in abundance, many algae grow about as well in darkness as in light; indeed, there are some forms that grow more luxuriantly as saprophytes in darkness than as autophytes in the light. The abundant growth of algae in water pipes and in drains doubtless is due to their capacity for saprophytism. Some algae, especially those occurring in lichens, almost equal the fungi in their saprophytic potentiality, being able to utilize such proteins as peptones for food.

In addition to the colorless algae noted above there are known a number of forms which lose their pigment when grown in media rich in organic food (as in strong glycerin solutions), the colorless condition ensuing either in darkness or in sunlight. Thus many green algae, blue-green algae, and diatoms are representative mixophytes, having on the one hand a capacity for independent existence, and on the other a possibility of saprophytism comparable to that habitually exhibited by fungi. Such phenomena show that the presence of chlorophyll

indicates rather the possibility of complete autophytism than its actual existence. The autophytic bacteria also are capable of living saprophytically, and hence are representative mixophytes.

Saprophytism in the seed plants. — The views of botanists as to saprophytism in the seed plants often have been altered, and even now the paucity of experimental data makes anything like a definite statement quite impossible. The first view was that all plants without chlorophyll are parasites. When it was discovered that the roots of *Monotropa* (fig. 411) are not connected with the roots of green plants, the term saprophyte was used to distinguish such plants from true parasites, which always are attached to other plants. Afterward it was discovered that the roots of *Monotropa* usually are completely enveloped by fungi, which act in an intermediary capacity between the seed plant and the humus, so that once more *Monotropa* is, perhaps, to be regarded as parasitic, though on fungi rather than on roots (see also p. 307). Similarly, all of the higher plants (except possibly the West Indian orchid, *Wullschlaegelia*) that commonly have been regarded as saprophytic, such as *Corallorhiza* and many other orchids (fig. 415), and such as the gametophytes of *Lycopodium* and *Botrychium*, have symbiotic relations with fungi and probably are parasitic rather than saprophytic; however, in such orchids as *Corallorhiza* partial saprophytism still seems a possibility, especially since the fungi occur within the root. The term *symbiotic saprophytism* has been applied to this phenomenon to express the double relationship, namely, the symbiotic relation between the fungus and the higher plant, and the saprophytic relation between the fungus and the soil (see further, p. 314).

While the supposedly saprophytic seed plants and pteridophytes appear, in reality, to be parasites, a capacity for saprophytism has been found to exist in various ordinary green plants. Long ago it was supposed that the luxuriant development of plants in humus is due to the absorption of organic food, but later this view was abandoned, the luxuriance being referred to various factors, such as the high water content, the abundance of nitrates, and the beneficial activities of earthworms, fungi, and bacteria. However, it has been discovered that when maize is grown in glucose or in invert sugar with its leaves in air which is devoid of carbon dioxide, sugar is absorbed by the root hairs and is utilized directly in the manufacture of starch. In such an experiment the maize behaves as a holosaprophyte, and it may be a partial saprophyte in ordinary cultivation, although the roots appear to absorb very

little organic food when the conditions are favorable for autophytism. It has been claimed, but scarcely proven, that root hairs secrete enzymes, as do fungi. Results similar to those obtained in maize have been reported in the vetch, the cress, and the radish, and it is very probable that many if not most green plants have a greater or less capacity for partial saprophytism.

Some seed plants (principally among the Scrophulariaceae) that commonly are partial parasites (p. 287) are said to be saprophytic in some cases; for example, *Melampyrum* develops haustoria among dead leaves and becomes attached indifferently to dead or to living roots. Even those species which become attached only to living hosts continue to derive nourishment therefrom after the latter are dead. *Lathraea*, which commonly is a holoparasite (p. 288), sometimes lives as a saprophyte. It has been claimed that certain mosses with few leaves (as *Buxbaumia*) are partially saprophytic; apart from the sparse foliage, the only argument for this view is the fact that the rhizoids penetrate among dead leaves and sometimes have knoblike processes resembling haustoria.

While much is yet to be learned about saprophytism in the seed plants, it certainly is an odd circumstance that the plants least likely to exhibit saprophytism are forms like *Monotropa*, which once were regarded as holosaprophytes, while saprophytism is best evidenced in such plants as maize, which has been regarded as a representative autophyte. However, the nutritive evolution of heterotrophic seed plants as a class seems rather to have been in the direction of symbiotic saprophytism (p. 314).

The origin of saprophytism. — The prevalent conception of the origin of saprophytism is that from time to time saprophytic branches have diverged at various levels from the main autophytic trunks. The saprophytic fungi and bacteria do not appear to form an independent and connected genetic line, but occur as disconnected groups, some of which resemble algae of widely different families. For example, in form and structure and in method of reproduction the bacteria resemble the blue-green algae, differing from them chiefly in the general absence of food-making pigments and in their much smaller size; the close relationship between these groups is emphasized further by the great saprophytic capacity of the blue-green algae, by the pigmentation of certain bacteria and fungi,[1] and by the fact that various

[1] Notable among the pigmented forms are the purple bacteria, which contain, in addition to the purple pigment, a green pigment that resembles chlorophyll. *Monilia sitophila*, a fungal form, is colorless when grown in the dark, but when grown in the light, it exhibits an orange color due to carotin.

bacteria are able to manufacture carbohydrates. Both among the bacteria and the blue-green algae there are unicellular, filamentous, and colony-forming species. The bacterial form, *Leuconostoc*, resembles the algal form, *Nostoc*, both in general appearance and in behavior. Similarly, the alga groups, Siphonales and Conjugales, show many resemblances to the fungus groups, Oomycetes and Zygomycetes, respectively (see Vol. One).

It is not difficult to picture the probable stages in the development of holosaprophytism and to imagine some of the possible underlying causes. Since the lower algae are mixophytes, saprophytism does not seem to involve the introduction of a new character, but chiefly the elimination of autophytism; probably there develops also an increased capacity for the utilization of organic food. The experiments previously cited appear to suggest that food-making by chlorophyll may be diminished or even checked in the presence of an excess of soluble carbohydrates. A second stage appears to be the gradual disappearance of chlorophyll, which also is associated with an abundant external food supply; this stage indicates the passage from partial saprophytism to temporary holosaprophytism. The final stage, the elimination of the possibility of chlorophyll formation and hence of autophytism, may be occasioned by the disappearance of plastids, but the factors involved in this are at present quite unknown.

Progressive variability in saprophytes. — While most saprophytic fungi and bacteria can be grown in various culture media, a sudden transfer to an unaccustomed medium results frequently in impaired activity or in death. However, if the change is made gradually through a series of intermediate solutions, successful cultures may result. For example, *Bacillus fluorescens putridus* ordinarily has its optimum growth conditions at 22° C, and can scarcely grow above 35° C; however, if media of gradually increasing temperature are used, a race is developed that grows vigorously at 41° C. Thermal bacteria, with an optimum of 37° C, can be treated similarly until they thrive at 66° C. Likewise, many saprophytes can be grown in toxic media if the poisons are increased gradually in successive cultures; in this way *Penicillium* can be grown ultimately in concentrated solutions of copper sulphate. Many forms, as *Aspergillus* and *Penicillium*, can be cultivated ultimately in salt solutions that are so highly concentrated as to produce plasmolysis or death if the transfer from ordinary media is made suddenly. Some forms secrete enzymes whose character

differs with the nature of the substratum, *Penicillium* even secreting a wood-destroying enzyme, hadromase, when grown on wood. Anaerobic bacteria may be accustomed gradually to the presence of oxygen, finally even thriving when it is present in considerable amount. Such phenomena, as a whole, have been called *accommodation*, the implication being that plants have the power of adapting or adjusting themselves to new situations. One of the most striking features of " accommodation " is the inability of saprophytes that have been grown for a long time under unusual conditions (*e.g.* at high temperatures, at high concentrations, or in toxic media) to thrive when they are suddenly transferred back to the ordinary media; in order to flourish in the latter, they must again be grown in a series of intermediate solutions of gradually decreasing temperature, concentration, or toxicity.

While the phenomena of " accommodation " are not well understood, no explanation is given by referring them to adaptation or adjustment (see p. 465). If a fungus is transferred to a salt solution of slightly higher concentration, the solute enters the plant and water passes out, tending to establish an equilibrium. If a series of like transfers is made to media of progressively greater concentration, similar processes take place, until finally the concentration within the fungus becomes so great that it can thrive in a medium which would have brought about plasmolysis through sudden water withdrawal, if it had been placed therein at the outset. Similarly, when a transfer is made suddenly from a strong to a weak solution, water may enter so rapidly as to burst the fungus, although a series of transfers to progressively weaker solutions makes possible the gradual entry of water and the gradual exit of salts. Perhaps the behavior of saprophytes in solutions that are subjected to progressive changes in temperature or in toxicity also may be capable of a comparable explanation. In any event, it seems advisable to substitute the term *progressive variability* for accommodation and similar vitalistic expressions.

Phosphorescence. — A few plants, chiefly saprophytes, exhibit *phosphorescence*, the mycelium of *Agaricus melleus* and of a few other fleshy fungi often being luminous in the dark, especially in wet weather, if there is an abundant supply of oxygen. Certain bacteria associated with meat decay also are phosphorescent. The phosphorescence of decaying wood probably is due to fungi or to bacteria. Luminosity is thought to be of no value to plants, although it is of possible use to certain animals.

The distribution of saprophytes. — While light is a large factor in determining the distribution of green plants, it plays almost no part

in the holosaprophytes, whose abundance is determined chiefly by the amount of dead organic matter and by the degree of freedom from transpiration. Probably saprophytes culminate in mesophytic woods, where soil bacteria are abundant, and where numerous saprophytic fungi permeate the soil and the rotting trunks. There is also a characteristic saprophytic flora in the humus underlying ponds and swamps, and even in the dark abysses of the ocean. Both in the forest and in the ocean depths the saprophytes play a part of great import to all organic life; as the organisms of decay and as agents of nitrification they make much material available for other organisms, and their symbiotic relations with green plants also are most important.

Probably saprophytic fungi display their greatest luxuriance in old mines, where the decaying timbers furnish a rich supply of food. The mycelia spread abundantly over the surface of the wood as well as within, and even far out on the adjoining rocks, the hyphal strands remaining connected with the source of food. Undoubtedly the uniformly high humidity is the chief factor in determining this astonishing luxuriance; that this factor is not darkness is shown by the fact that similar rich cultures may be obtained in the light on bread or on cheese enclosed in moist chambers. In caves, where there are no timbers, saprophytes often luxuriate, the necessary organic matter being supplied by streams entering from the outer world, by the excrements of cave animals (as the blind fish), and of cave-frequenting animals (such as bats), and even by tallow dropped from the candles of human visitors. Were it not for the saprophytes, ocean depths and caves would be essentially devoid of plant life.

2. PARASITISM

General considerations. — *Definitions.* — *Parasites* are plants or animals that derive foods or food materials from other plants or animals to which they are attached. A *holoparasite* is one that is entirely dependent for its food upon the organism to which it is attached, common illustrations being parasitic fungi, broom rapes, and parasitic animals. A *partial parasite* is one that is only partially dependent upon the organism to which it is attached, being capable of manufacturing a part or even all of its food; in the former case it derives food from its host, in the latter case only food materials. Representative partial parasites are the mistletoe and many of the Scrophulariaceae.

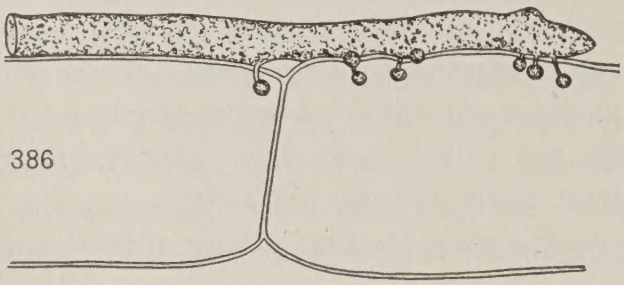
Intergradations. — All possible gradations connect partial parasites with holoparasites; the former also grade similarly into autophytes and partial saprophytes, and the latter into holosaprophytes. The mistletoe, like the autophytes, probably makes its own carbohydrates, differing from them chiefly in taking its water and salts from a host plant instead of from the soil; such a plant is termed a *water parasite.* Colorless parasites take organic foods from their host plants; even among these there probably are degrees of parasitism, some manufacturing proteins, while others absorb them along with carbohydrates. Gradations between autophytes and partial parasites are best illustrated by the Scrophulariaceae, and are described below. There are many fungi and bacteria that can exist either as holosaprophytes or as holoparasites; such forms are called *facultative saprophytes* or *facultative parasites*, in contrast with *obligate saprophytes* (as most molds) and *obligate parasites* (as the more familiar phases of rusts and smuts).

Various bacteria that ordinarily are saprophytic become parasitic when several successive generations are grown on carrots or turnips. The fungus, *Empusa*, infects living flies, causing their death, but it grows with undiminished vigor after the death of the host. Similarly, a species of *Saprolegnia* causes the death of fishes, continuing to live afterward as a saprophyte. Various parasitic bacteria are capable of saprophytic existence, and a number of the fungi causing plant cankers, stem rots, and leaf spot diseases also may live as saprophytes; some of the latter are regularly saprophytic in their later stages. The common saprophytic mold, *Mucor mucedo*, causes a destructive rot in sweet potatoes. Similarly, no sharp lines of demarcation separate saprophytic and parasitic timber fungi. Most smuts and rusts have alternating stages of parasitism and saprophytism. Even among the seed plants there are a few forms which usually are parasitic, but which seem capable of partial saprophytism, notably *Lathraea* and *Melampyrum*, the latter also having a capacity for autophytism. In many cases parasites, while attached to living plants, do not come into contact with living cells, secretions from the invading fungus killing the cells before any of the contents are absorbed. In water parasitism (*e.g.* in the mistletoe) the dead hadrome of the parasite is in contact with the dead hadrome of the host. Yet the latter instances properly belong to the phenomena of parasitism, since the host plants are injured and are deprived of materials which otherwise they might have used.

Parasitic fungi and bacteria. — *General characteristics.* — The best-known parasitic bacteria are the *pathogenic* forms, which occasion many diseases in man and in other animals, and also in plants, for example, the organisms causing tuberculosis, cholera, and typhoid fever. These forms generally are less differentiated than are the

saprophytic bacteria, perhaps giving an illustration of reduction from a more specialized ancestry. Some bacteria that apparently are parasitic are not pathogenic, such as *Leptothrix* and *Sarcina*, which live respectively in the mouth and the stomach. *Bacillus radicicola*, the species that forms galls on legume roots (p. 303), also lives saprophytically in the soil, and thus is a facultative form.

The mildews, rusts, and smuts are representative parasitic fungi, most of which are deleterious to their host plants, some species producing conspicuous galls in various organs. Some of the Polyporaceae (as the bracket fungi) are harmful parasites on trees. The hyphae of parasitic fungi are thought to be more specialized than are those of saprophytic forms, having greater power of penetration into woody and mechanical tissues, and it is likely also that their absorptive efficiency is greater. The penetrative power of the hyphae is due in large part to the substances which they secrete, particularly various enzymes, such as the wood-destroying enzymes of the tree-inhabiting fungi. Wounds of various kinds greatly facilitate the invasion of plant organs by parasites. While ordinary hyphae often invade the living host cells, in many cases they creep along the outer surface (as in various mildews) or penetrate between the cells, special branches known as *haustoria* piercing the walls (especially through the pits) and absorbing the contents of the lumina; surface forms are known as *ectoparasites*, while internal forms are termed *endoparasites*. In *Albugo* the haustoria are knoblike processes (fig. 386) and in *Peronospora* the haustorial branch



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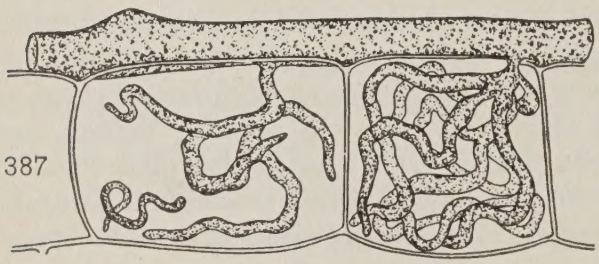

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FIGS. 386, 387. — Haustoria of parasitic fungi. 386, a hyphal filament of *Albugo candida* from which there originate small spherical haustoria that penetrate the parenchyma cells of the host plant, *Lepidium sativum;* 387, a hyphal filament of *Peronospora calotheca* from which there originate richly branching haustoria that penetrate all parts of the parenchyma cells of the host plant, *Asperula odorata;* both figures highly magnified. — From DEBARY.

may divide into a number of finger-like absorptive organs (fig. 387). The spores of most parasitic fungi, even of such obligate forms as the rusts, germinate somewhat readily in a number of media, thus differing from the seeds of the higher holoparasites; oddly enough the spores of many saprophytic fungi germinate much less readily.

Heteroecious and autoecious parasites. — If a parasitic fungus has but a single host in its life history, it is called *autoecious*, while if different stages occur habitually on different hosts, it is called *heteroecious*. In the smuts there is an alternation of saprophytic and parasitic phases, but in the heteroecious rusts, in addition to a similar alternation, the parasitic phase is partly on one host and partly on another. Representative heteroecism is illustrated by the wheat rust, *Puccinia graminis*, whose saprophytic phase occurs in spring, when the resting spores, known as *teleutospores* (fig. 433), germinate on the ground, and give rise to a mycelium, which produces *basidiospores*. If any basidiospores, scattered by the wind, chance to fall on a barberry leaf, a parasitic mycelium is developed, which in turn produces spores known as *aecidiospores*. If these spores are carried by wind to wheat leaves, they develop into a mycelium which in summer gives rise to reddish spores, the *uredospores* (fig. 431), which also germinate on wheat leaves. Later in the season the same mycelium gives rise to black, thick-walled teleutospores (figs. 432, 433), which fall to the ground and remain dormant until spring. Another well-known heteroecious fungus is *Gymnosporangium*, whose aecidial stage occurs on *Pyrus* or on other Rosaceae, while the teleutospore stage occurs on *Juniperus*, causing the galls known as cedar apples.

One of the most remarkable features of the heteroecious rusts is their diverse behavior. In some species of rusts certain stages are habitually lacking; for example, the *uredo* stage may be absent, and sometimes the *teleuto* stage also, the life history then consisting solely of *aecidial* and saprophytic stages. Again, the aecidial stage may be absent, as in *Puccinia malvacearum*, resulting in an alternation of the saprophytic and the uredo-teleuto stages; or both the aecidial and uredo stages may be wanting, the basidiospores giving rise directly to a teleutospore mycelium. Moreover, there are strictly autoecious forms, such as *Puccinia asparagi*, in which the aecidial stages and the uredo stages develop from the same mycelium. Still more interesting are the variations within a single species. The wheat rust, for example, thrives in regions where the barberry does not exist, partly because the uredo mycelium even in very cold climates is able to hibernate in winter wheat, thus eliminating the necessity of either saprophytic or aecidial stages, and partly because uredospores that have survived the winter may infect young wheat the following spring; even the teleutospores or basidiospores may directly infect young wheat in certain instances. In tropical climates *Uromyces fabae*, a parasite of *Vicia faba*, spreads solely by uredospores. Thus heteroecism is seen to be in part facultative; it is obligate, however, in certain cases, as in *Coleosporium melampyri*, whose host is an annual.

Sometimes it has been thought that the ease with which rusts make new infections cannot be explained merely by their remarkable variability. Consequently it has been suggested that under certain conditions the protoplasm of the fungus and the host may merge into a common *mycoplasm*, and in this invisible or imper-

fectly evident form, the fungus is thought to exist in the seed. When the seed germinates, the fungus is supposed once more to become differentiated into an obvious mycelium. This strange theory of the mycoplasm was formulated to account for cases of parasitism, in which all evident external sources of infection are lacking. Such a theory, appearing to defy the possibility of experimental analysis, like the theories of vitalism and of adaptation, should be resorted to, if at all, only after all other tenable hypotheses have been overthrown. Infection through seeds is much more likely to result from spores intimately associated with them than from mycoplasm; indeed, mycelia with uredospores and teleutospores have been observed just beneath the bran layer in wheat grains that were produced by plants badly infected by rust, and nests of hyphae have been seen even in the embryo.

Physiological species and progressive variability. — Some species of parasitic fungi (*e.g. Botrytis cinerea*) may live on two or more hosts, and hence are known as *plurivores*, while those that are confined to a single host plant are termed *univores;* a familiar instance of the latter is seen in the corn smut, *Ustilago maydis*. In many rusts, in some mildews, and in the ergot, species that appear plurivorous have, in a sense, been found to be univorous. For example, *Puccinia graminis* is in reality a complex of forms morphologically alike but physiologically dissimilar; common forms referred to this species occur on rye, oats, and various other grasses, as well as on wheat. However, uredospores from the oat rust will not infect rye, nor *vice versa*, though their aecidial stages, as well as that of the wheat rust proper, occur on the barberry. Even aecidiospores which have developed from an ancestry that has grown on oats will not grow on rye, nor *vice versa*. Forms that thus are alike morphologically but unlike physiologically are known as *physiological species*, and the phenomenon is called *specialization*. The true wheat rust (*Puccinia graminis tritici*) is much more *generalized*, growing readily on barley, oats, and rye, as well as on wheat. As a rule the uredo and teleuto stages of a rust are much more specialized than are the aecidial stages.

The common view regarding physiological species is that the generalized forms are the more ancestral; for example, the specialized oat rust (*Puccinia graminis avenae*) and the rye rust (*P. g. secalis*) are supposed to have been derived from the more generalized wheat rust (*P. g. tritici*) by progressive variability on a special host. There is experimental evidence for this view. For example, *Puccinia smilacearum digraphidis* is a plurivorous species, whose uredo and teleuto stages occur on *Phalaris arundinacea*, while the aecidial stage occurs indifferently on various Liliaceae; however, after the aecidial stages were cultivated for ten years solely on *Polygonatum multiflorum*, a univorous form was produced.

It is possible to induce variations leading to greater generalization as well as to greater specialization. Comparable to the rusts in many respects is *Erysiphe*

graminis, one of the mildews which has many physiological species. While the spores from one physiological species ordinarily do not infect the host of another, they may do so, if the host is wounded; for example, rye, which usually is immune to wheat mildew, is susceptible if cut or bruised. Much more significant is the rôle of the *bridging hosts*. Spores from that form of *Erysiphe graminis* that is parasitic on *Bromus commutatus* do not directly infect *B. mollis*, but if *B. hordeaceus* is used as a *bridge*, that is, if spores from the parasite of *B. commutatus* are used to infect *B. hordeaceus*, the spores developing on the latter readily infect *B. mollis*, which otherwise is immune to this particular parasite. Similarly, by the use of certain hosts as bridges, the ordinary host range of various forms of *Puccinia graminis* may be extended; for example, barley serves as a bridge from oats to rye or to wheat, or from rye or wheat to oats. While *Erysiphe graminis* is made up of highly specialized races, a related species, *Erysiphe cichoracearum*, is a generalized form; spores of this species that develop on one of the Cucurbitaceae readily infect not only other Cucurbitaceae, but even plantains and sunflowers. Interesting tendencies away from specialization are furnished also by certain parasites that have attacked new hosts, when one or the other is introduced from foreign countries. For example, *Puccinia malvacearum*, which was introduced from Chile to Europe with a cultivated *Althaea*, has spread to species of *Malva*. The aecidial stage of *Cronartium ribicola*, a parasite of the European *Pinus cembra*, has become a destructive parasite on *P. strobus*, which was introduced into Europe from America. One of the most remarkable of plurivorous rusts, in view of the generally close relationship of the hosts of any given parasite, is *Cronartium asclepiadeum*, a common parasite on *Vincetoxicum*, one of the Asclepiadaceae, which is equally at home on the peony, one of the Ranunculaceae; it has become parasitic also on *Nemesia versicolor*, one of the Scrophulariaceae; the systematic relationship of host plants is of significance to parasites only as it happens to involve similarity in the physical or chemical character of the substratum.

The factors involved in progressive variability among the parasitic fungi are quite unknown, and doubtless are much more complicated than among saprophytes, where the culture media may be relatively simple, and capable of analysis. However, it is to be believed that the explanation will be along similar lines, and that it need not involve the mysticism which is inherent in the accommodation theory.

The origin of parasitism in fungi and bacteria. — Parasites appear to be more highly specialized than saprophytes, and most parasitic fungi and bacteria probably have arisen from algae by way of saprophytism; among the thallophytes there are many transitions between mixophytes and holosaprophytes, and between the latter and holoparasites, but few, if any, between mixophytes and holoparasites.[1] The

[1] There are a few parasitic algae that may have developed directly from mixophytes into parasites rather than by way of saprophytism. One of the most interesting of these parasitic algae is the destructive tea rust, *Cephaleuros virescens*. Another parasitic alga is *Rhodochytrium spilanthidis*, which grows on *Ambrosia* and on other hosts. There are also a number of marine red algae that are parasitic; among these is *Choreocolax polysiphoniae*, which is completely colorless and has plasmatic connections with its algal host.

probable stages in the origin of saprophytism have been mentioned. The next step, namely, the development of facultative parasitism, seems to follow easily, and is illustrated by many existing species (p. 277). The succeeding stage probably is that of obligate parasitism, involving the loss of a capacity for saprophytism. Doubtless there are degrees of parasitism even among the obligate parasites, since some species (as *Pythium de baryanum*) soon cause the death of the host and hence their own death. The rusts, which rarely kill their host plants, appear on this account to exhibit a higher stage of parasitic evolution. Another possible stage, still further removed from autophytism, is illustrated in the univorous habit; it has been noted that univores may arise from plurivores through progressive variability, and that a return to a plurivorous condition is equally possible.

Probably the most complicated situation of all is afforded by heteroecism, and no species has been so much discussed in this connection as the wheat rust. This species may once have had all stages both on the barberry and on wheat; if the aecidial stage developed poorly on the wheat and the uredo stage poorly on the barberry, each ultimately may have become eliminated on those hosts, resulting in the present heteroecious state. Another conception regarding the wheat rust is that the barberry was the original host, and that by mutation or otherwise the uredo and teleuto stages came to develop on various grasses; this view is favored by the greater generalization of the aecidial stage. A possible mode of evolution of physiological species is suggested by *Puccinia hieracii*, a rust that infects a great many species of *Hieracium*. It appears that each infected species of the latter is characterized by a physiological species of the former. There is evidence that the evolution of the species of *Hieracium* is very recent, and it is believed that the physiological species of the rust have developed with the species of the host.

Chemotropism is thought to have some connection with the origin of parasitism. All fungi are prochemotropic with reference to certain substances, and apochemotropic with reference to others. For example, most saprophytes and facultative parasites grow toward saccharose. The notably plurivorous parasite, *Botrytis cinerea*, though prochemotropic with reference to saccharose, does not penetrate apples, because it is apochemotropic with reference to malic acid. The fact that parasitic hyphae grow toward decoctions of their host plants suggests the likelihood of chemotropic relations. *Penicillium*, a representative saprophyte, grows in living tissues if the latter are injected with substances to which *Penicillium* reacts prochemotropically. *Trichothecium*, another saprophyte, when grown for twelve or fifteen generations on begonias that have been injected with sugar, is able thenceforth to

continue as a parasite without such injection and to bear fruit in the usual manner. Similarly, certain parasites may be made to infect new hosts, if the latter are thus injected.

The chemotropic theory of parasitism would regard obligate parasites as forms that react only to substances that are found in living plants, and univorous parasites as forms that react only to substances that are found in a single host species. This theory is not universally accepted, but no more tenable hypothesis has been suggested. In all theories of parasitism, especially in those that attempt to account for the phenomena of heteroecism and specialization, it is difficult to explain the fixation of new habits, inasmuch as there is no evidence that variability is ever lost. Hence appeal often is made to mutation as the decisive element in determining the origin of the forms.

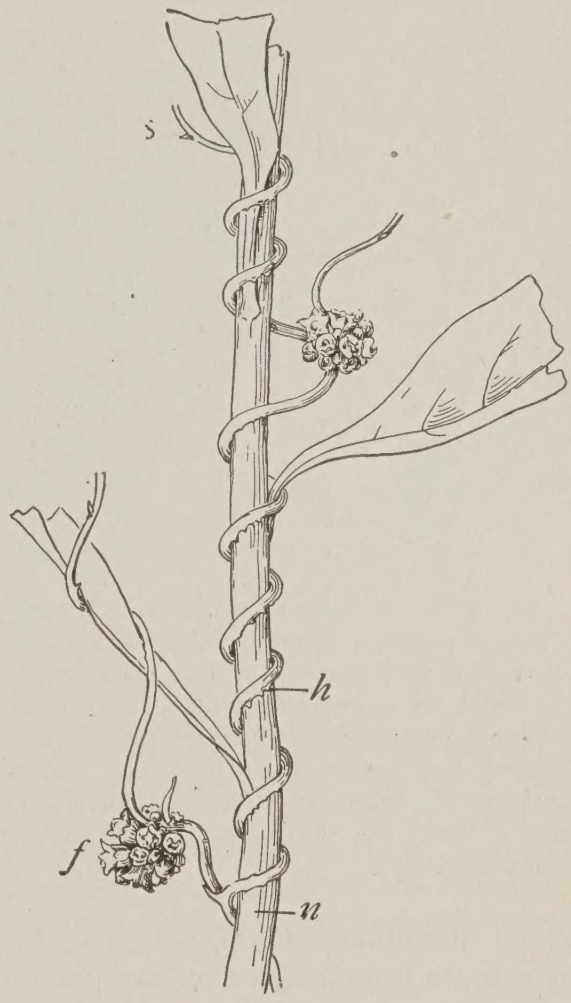


FIG. 388. — A portion of a shoot of a dodder (*Cuscuta gronovii*), a sinistrorse twining parasite; note the haustoria (*h*) which penetrate the tissues of the host plant (*n*); the leaves (*s*) are minute scales; *f*, flowers.

Immunity and related phenomena. — Most cultivated plants are subject to bacterial or fungal diseases. In many species certain varieties are particularly subject or *predisposed* to infection, whereas other varieties are *disease-resistant* or *immune*. Few phenomena are more puzzling than are those of immunity; in many cases it may be attributed to the absence of substances that induce prochemotropic reactions, or to the presence of substances which either induce apochemotropic reactions or neutralize the enzymes secreted by the fungus. In addition to factors of a chemotropic nature, immunity has been referred to the presence of an impenetrable epidermis, to the secretion of antitoxins, and to the absence of the proper food for the parasite.

Some forms, as *Penicillium italicum* and *Pseudomonas destructans*, secrete toxins poisonous to themselves, thus making the host plant immune through their own activity. Immunity of this character is experienced commonly by many plants and animals that have been subject to certain bacterial diseases. In some cases "disease-resistance" involves very complicated phenomena; for example, when the olive is infected by *Bacterium oleae*, there are developed in the host plant layers of sclerenchyma and cork that isolate the bacteria, and antibodies are formed which are specifically toxic to the bacteria. In the lack of all obvious determining factors, appeal sometimes has been made to inherent hidden differences between the various members of a given species, but this "explanation" fails to explain. In any case, immunity is not always or even usually due to the failure of spores to germinate, since parasitic fungi often are found in various early stages of development on plants which are immune to effective parasitism.

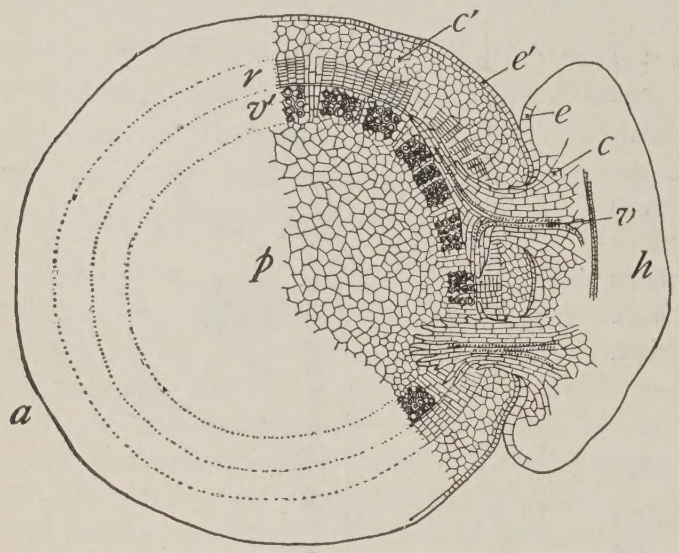


FIG. 389. — A longitudinal section through two haustoria of a dodder (*Cuscuta gronovii*) and a cross section of the stem of the host plant which they are penetrating; note that the vascular tract (*v*) of the parasite with its hadrome comes into contact with the same region (*v'*) in the host; *p*, central pith of the host; *c*, cortex of the parasite; *c'*, cortex of the host; *e*, epidermis of the parasite; *e'*, epidermis of the host; *r*, cambium of the host; highly magnified.

Parasitic seed plants. — *General features.* — Parasitic seed plants, while relatively few in number, are of remarkable interest. A familiar holoparasite is the dodder (*Cuscuta*), whose yellowish stem twines closely about that of the host plant (fig. 388), into which many haustoria penetrate (fig. 389). Among the important holoparasites are the Orobanchaceae, a family of root parasites, one of the most interesting of which is *Orobanche fasciculata*, a frequent parasite on *Artemisia* (fig. 390); in this species there is but a single point of attachment, which may be on a small lateral root at some distance from the

main stem axis of the host. Perhaps the extreme of holoparasitism is found in the tropical families, Rafflesiaceae and Balanophoraceae, in many of which the vegetative body of the parasite is entirely within the host, so that the plant is in evidence only when in blossom; the largest known flower, which sometimes is a meter in diameter, belongs to one of these, *Rafflesia arnoldii*. Among the commoner partial

FIG. 390. — Individuals of a holoparasite, *Orobanche fasciculata*, attached to the roots of an *Artemisia;* note the stages between young seedlings which appear like root swellings and adult plants with opening flowers; note also that the parasite is attached to the host at but a single point; Gary, Ind. — Photograph by FULLER.

parasites are various mistletoes (as *Viscum* and *Phoradendron*, fig. 391) and a large number of the Scrophulariaceae, especially in the tribe Euphrasieae (as *Melampyrum*, *Rhinanthus*, and *Euphrasia*); all such plants differ from the holoparasites in containing chlorophyll.

Holoparasitic seed plants differ from their autophytic relatives not only in the presence of haustoria and in the absence of chlorophyll, but also in the relative absence of leaves, whose place is taken by insignificant and probably functionless scales. As among fungi, the higher holoparasites may be plurivores (*e.g. Cuscuta gronovii*) or univores;

examples of the latter are the flax dodder (*Cuscuta epilinum*) and *Orobanche hederae*, a parasite on the English ivy. The European mistletoe, *Viscum album*, usually is regarded as a plurivore, but the presence of physiological species is suggested by the fact that the fir mistletoe does not grow on the pine, nor *vice versa;* the form that infests deciduous trees also appears to be distinct from the forms that parasitize the conifers. Even plurivorous species of *Cuscuta* grow very differently on different hosts, the number of forms on which they flower

A *B*

FIG. 391. — The mistletoe, a partial (water) parasite: *A*, spiny honey-locust trees (*Gleditsia triacanthos*), many of whose limbs are infested with mistletoe (*Pheradendron flavescens*); *B*, a close view of a single mistletoe plant; Rome, Ind. — Photographs supplied by LAND.

and fruit being much less than the number on which they can develop vegetative organs.

Haustorial structures. — The haustoria of parasitic seed plants are much more complex than are those of the fungi, involving various elements in the cortical and vascular tissues. The simplest haustoria occur in such partial parasites as the Euphrasieae, where contact with the host often seems more or less casual. In the mistletoe, also a partial parasite, but more specialized, the haustoria are prominent organs which exhibit some structural complexity, their hadrome elements coming in close contact with similar elements in the host. Still more specialized are the haustoria of *Cuscuta* (fig. 389) and of *Orobanche*, their terminal cells deploying in all directions, and coming into such close contact with the host cells that sometimes it is difficult to distinguish one from the other, though the frontier cells of the parasite

commonly are richer in starch than are the adjoining cells of the host; particularly in *Orobanche* are the cortex, leptome, and hadrome of the haustorium in contact, respectively, with the cortex, leptome, and hadrome of the host. Perhaps the acme of specialization is seen in *Pilostyles*, where the haustorial elements permeate the host tissues like fungal hyphae.

The rôle of haustoria. — The haustoria of parasitic seed plants resemble those of fungi in the method of penetration. In the mistletoe the pressure exerted by the developing haustorium results in the penetration of weak spots, such as lenticels, bark rifts, and cellulose walls; some holoparasites (as *Orobanche* and *Cuscuta*) also secrete substances that dissolve the cell walls of the host. In *Lathraea* the outer haustorial layer is glandular, secreting a cement, which enables the parasite to adhere to the host.

The actual substances absorbed by haustoria are inadequately known. In *Cuscuta* careful cultures indicate that glucose is the chief substance taken from the host, but since the sieve tubes of the host and of the parasite are in contact both in *Cuscuta* and in *Orobanche*, it generally has been assumed that proteins are absorbed also. The haustoria of such holoparasites secrete diastases (such as amylase and cellulase), which digest the starch and similar foods of the host. In the mistletoe it is obvious that foods or food materials are taken from the host tree. Because of the hadrome contact and the green leaves, the usual assumption is that food materials (*i.e.* water and salts) are the chief things absorbed; hence such plants have been called water parasites.

In spite of the possibility that the chlorophyll may not play its usual rôle, this assumption probably is correct, inasmuch as cultures in weak light result in impoverished individuals. However, the obvious harm caused to trees by the mistletoe, the fact that it does not grow on dead trees, and the fact that some mistletoes (as *Arceuthobium*) are essentially holoparasitic, give some support to the view that the green mistletoes may get certain foods parasitically.

Of special interest are the Euphrasieae, since, in addition to haustoria and leaf chlorophyll, there are root hairs which are attached to soil particles. Careful experiments have shown that in this group there exists every gradation from autophytism to holoparasitism. Nearly all species have chlorophyll and all have haustoria, thus appearing to indicate a double nutritive potentiality. At one end of the series is *Odontites verna*, which can pass its entire life cycle as an autophyte,

producing seeds capable of germination; and almost at the other end is *Tozzia*, a plant without root hairs which requires root contact for germination, and which lives nearly two years as a subterranean holoparasite before sending up a green aerial shoot that lives but a few weeks. At the extreme end of the series is the holoparasite, *Lathraea*. The more autophytic species have abundant root hairs and few haustoria, while the more parasitic species have few root hairs and abundant haustoria, culminating in forms like *Tozzia* and *Lathraea*, which have no root hairs, and in which haustoria develop even in early seedling stages. Thus there is a reciprocal relation between root hairs and haustoria that probably indicates the degree of parasitism.

While the parasitism of the Euphrasieae is undoubted, the substances obtained from the host plants are unknown, except in such forms as *Tozzia* and *Lathraea;* from analogy with the mistletoe, it might be thought that they absorb water and salts from the host plants, a view that is supported by the reciprocal relation of root hairs and haustoria. In favor of the view that carbohydrates are absorbed is the fact that some forms (as *Melampyrum pratense*) are supposed to have a capacity for saprophytism, and that many ordinary green plants are partial saprophytes. It has been claimed that in some species (as *Euphrasia officinalis*) the chlorophyll has almost if not quite lost its food-making power; this view, however, seems somewhat improbable, since all forms except *Lathraea* require light for their optimum development, and since most species grow more luxuriantly as autophytes in the light than as parasites in the shade; furthermore, careful experiments show that starch formation in these partial parasites bears quite the same relation to abundant light and carbon dioxide and to open stomata as in autophytes. In any event, the fact that all of the Euphrasieae studied, even the most autophytic, grow more luxuriantly with than without parasitic attachment shows that something is gained through parasitism, but it must remain for further experimentation to determine its exact nature.

The influence of external factors upon development. — The seeds of autophytes germinate in the presence of oxygen under proper conditions of temperature and moisture, but those of extreme holoparasites, such as *Orobanche*, require still another condition, namely, contact with the proper host plant; this condition probably means a particular kind of chemical stimulation. *Cuscuta*, though commonly a holoparasite, germinates readily in ordinary soil, and thus its parasitism appears to be less complete than is that of *Orobanche;* this view is supported also by the occasional presence of chlorophyll and by its less specialized haustoria. Even in *Cuscuta* there are degrees of parasitism, some species (as *C. lupuliformis*) germinating readily and living independently for some time, whereas other species (as *C. europaea*) germinate

slowly and soon die if a host plant is not present. The seeds of partial parasites, as in the Euphrasieae, germinate generally in ordinary soil, though host contact seems to facilitate germination; *Tozzia*, however, requires host contact for germination, in this respect alone appearing to surpass the dodder in parasitic specialization. The seeds of *Aeginetia*, a relative of *Orobanche*, require host contact for germination, the roots of many plants serving equally well. Upon germination peculiar hair tendrils arise, and further development depends upon their coming into contact with the roots of certain monocotyls.

In some partial parasites (as *Melampyrum pratense* and *Santalum*) haustoria appear to originate without special contact stimuli, though their full development usually requires contact with a living host; for example, in *Melampyrum*, tracheids become differentiated only after such contact. In holoparasites (as *Cuscuta* and *Lathraea*) and probably in most partial parasites (*e.g. Odontites*), even the first stages of haustorial development require contact with a living host. That the question is not merely one of contact, however, is shown by the fact that non-nutritive solid bodies do not stimulate haustoria. It has been claimed that when an *Epifagus* plant comes in contact with a beech root, haustoria develop in the host rather than on the parasite. Probably the factors involved in haustorial stimulation are chemical in nature and exceedingly complex.

In the Euphrasieae many of the species exhibit a high degree of variability, the amount and character of which depends upon the conditions to which they are exposed. As previously noted, some of this group (as *Lathraea*) may be either saprophytes or parasites, and others (such as species of *Melampyrum* and *Odontites*) may exhibit varying degrees of saprophytism, parasitism, and autophytism. When *Odontites verna* is grown in humus, only 10 per cent of the plants are attached to hosts, and yet the plants are more vigorous than in sand, where 43 per cent exhibit parasitic attachment. Parasitic Euphrasieae are much more luxuriant on vigorous hosts than on weak hosts, developing larger seeds and having larger, healthier, and more autophytic progeny. The progeny of weak parasites is much more likely to be albescent than is the progeny of strong parasites. The latter phenomena are very suggestive from an evolutionary standpoint. The culmination of variability appears to be in *Alectorolophus*, where many so-called species have been found experimentally to be merely habitat varieties.

Holoparasites are much more specialized, and are more completely dependent upon their hosts than are partial parasites; hence they exhibit much less variability. However, *Cuscuta* shows interesting variations which indicate that probably it has not reached the utmost bounds of parasitism; for example, *Cuscuta monogyna* has been grown to maturity as a saprophyte in glucose solutions. While the presence of plastids in *Cuscuta* has been both affirmed and denied, there is little doubt

of the presence of chlorophyll when the dodder is grown in the shade or on starved hosts; indeed, there is evidence that the dodder is able to manufacture small quantities of carbohydrate food. *Cassytha*, a member of the Lauraceae, is a parasite of similar aspect, and likewise is yellow in the sun and green in the shade. When *Cuscuta* grows on members of the Solanaceae, the haustoria secrete an oily substance not noticeable elsewhere; since the poisonous alkaloids of the Solanaceae do not enter the parasite, it has been suggested that the haustorial secretions may have the nature of an antitoxin. Certain plants appear to be immune from parasitic attack, possibly through the secretion of toxins, or of substances which induce apochemotropic reactions in haustoria, or through the absence of substances which induce prochemotropic reactions (*e.g.* glucose, in the case of *Cuscuta*). When the pear is attacked by the mistletoe, the infected branches soon die, whereupon the mistletoe dies; thus the pear generally is free from this parasite. Some trees are immune to parasitic attack through the impenetrability of the cork layer, and sometimes infected regions of host plants are isolated by cork formation.

The origin of parasitism in seed plants. — Whatever may be said of the fungi, the parasitic seed plants obviously form a series of disconnected groups, each of which is more or less clearly related to some autophytic group, near whose level the parasitic group in question probably originated. The Euphrasieae appear to be in a state of active evolution, and they exhibit all stages of gradation to autophytic Scrophulariaceae, a family to which they clearly still belong. The parasitic dodders are so close to the autophytic morning glories that usually they are regarded as belonging to a common family. Even the Orobanchaceae, while commonly accorded separate family rank, obviously are close to *Gloxinia*. *Rafflesia* and *Balanophora* are more remote from any known autophytic stock, and yet they are believed to be not very far distant from the Aristolochiaceae. In no case is there a long genetic series of heterotrophic forms, as in the fungi.

While thallophytic parasites probably have passed through an intermediate saprophytic stage, this may not have been the case in seed plants. An argument for such a saprophytic stage is furnished by facultative forms like *Lathraea* and *Melampyrum*, and also by the probable capacity of many ordinary autophytes for partial saprophytism. Yet such parasitism as that of the mistletoe, where only water and salts appear to be taken from the host, seems on the whole simpler than the saprophytic absorption of organic foods. Practically nothing is known concerning the exact causes underlying the development of parasitism in seed plants, and even the various stages cannot as yet be regarded as certainly known.

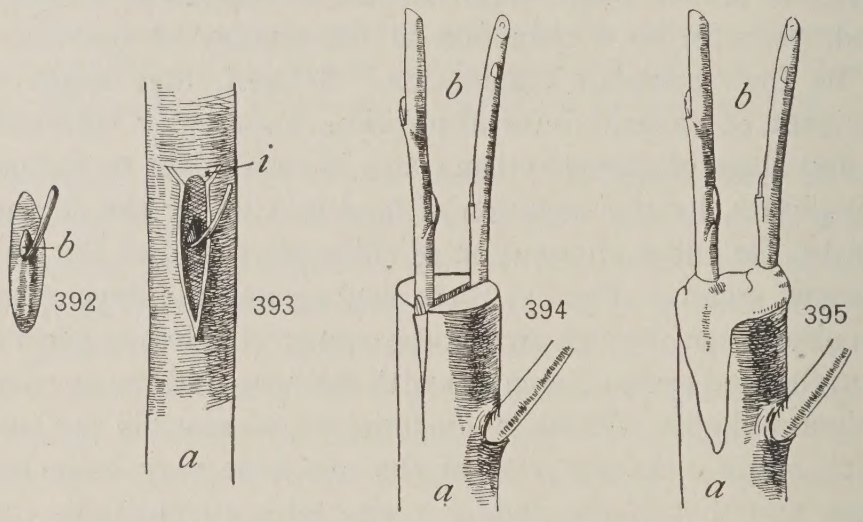
The intergradations among the Euphrasieae are very suggestive of possible stages in parasitism, and the following may be hazarded as a possible series in the development of such a root parasite as *Oro-*

banche. The roots of plants of different species frequently come in contact in the soil, and it may be supposed that the cells, either through mechanical causes or through chemotropic reactions, may come into sufficiently close contact to permit of osmotic interchange. Water or salts or both would then pass from regions of high to those of low pressure, the plant in which the pressure is low being the incipient parasite, while the other is the incipient host. If some substances exist in greater concentration in one plant and other substances in the other plant, the condition might give rise to reciprocal parasitism (p. 302). A second stage might be the development of haustoria, followed, perhaps, by a reduction in the number of root hairs and finally by their complete elimination. A third stage might be the development of carbohydrate absorption, apparently corresponding to the first stage of saprophytism; this in turn might be followed, as in thallophytes, by the cessation of food-making by the chlorophyll, or even by the entire elimination of chlorophyll and of the leaves as conspicuous organs. Finally, there might come the development of protein absorption through sieve tube contact, the loss of germinating power in the seed except in contact with the host, and the development of a univorous habit. Parasites on aerial organs scarcely can have had a similar origin; the ancestor of the mistletoe may have been an epiphyte, and that of the dodder a vine with adventitious climbing roots. In the tropics the mistletoe family has many parasitic representatives that are scarcely distinguishable from epiphytes, since they possess roots which spread over the bark of the host plants.

Attempts have been made to ascertain the factors involved in parasitism by growing one plant on another instead of in the soil. Peas have been grown on beans in such a way that they could obtain water and salts only from the latter; under these conditions they not only developed a root system within the artificial host, but reached maturity, producing flowers and even seeds capable of germination. Similar and equally successful experiments have been carried on for a much longer time in which a grape (*Cissus digitata*) has been used as the parasite and various cacti (as *Opuntia* and *Cereus*) as hosts. In this experiment the grape probably is a partial parasite comparable to the mistletoe, taking chiefly water and salts from the host and manufacturing its own carbohydrates. This conception is supported by the fact that the osmotic pressure of the cell sap of the grape was considerably higher than that of the cactus. In all cases studied the osmotic pressure of the sap of the experimental parasite surpassed that of the host.

Grafting. — *General phenomena.* — Closely allied to parasitism are the phenomena of *grafting*, a process in which a shoot or bud (the *scion*)

is inserted in another plant (the *stock*) in such a way that the former continues to grow through the use of food materials derived from the latter. Grafting is done in various ways, one being to place together oblique surfaces of stock and scion of about equal size, grafting-wax being employed to hold them in place and to give protection; or small scions may be inserted in a large stock which has been cut transversely (figs. 394, 395). *Budding* is a form of grafting in which a single bud remaining attached to a small piece of bark is inserted in a T-shaped incision in the stock (figs. 392, 393). The grafting of fruit trees is



FIGS. 392–395. — Budding and grafting: 392, 393, shield-budding, the name being derived from the shield-shaped piece of bark with the removed bud, *b*; 393, the stock in which a T-shaped incision (*i*) is made; the bud is then inserted and the whole tied securely; 394, 395, cleft-grafting; 394 represents two scions (*b*) wedge-shaped below, which are inserted into a cleft in the stock (*a*), and then fixed in place by grafting wax, as in 395. — From BAILEY.

of great commercial advantage, since most horticultural varieties do not reproduce true to seed, and since even those varieties which "come true" can be brought into bearing some years sooner by grafting than by growing from seed. In the Rosaceae, grafting commonly is possible only among closely related plants, as among the species of a common genus; for example, plums, peaches, and apricots may be readily intergrafted, as may apples, pears, and quinces, while intergrafting is impossible between apples and plums; sometimes closely related species cannot be intergrafted (*e.g. Prunus padus* and *P. laurocerasus*). In the Solanaceae and the Compositae many instances are known where different genera can be intergrafted, and cases are on record of intergrafting between different families. The latter phenomenon does not

seem strange, when it is remembered that successful grafting depends upon similarities between vegetative characters, and that these are not necessarily correlated with the reproductive characters upon which plant relationships are based.

At the juncture of the graft symbionts there is developed a callus, in which xylem and phloem elements arise, uniting the two plants so that they appear as one. However, in spite of the close union, the two plants in large part retain their individuality and are nearly as distinct from one another as are a parasite and its host. The scion may well be compared to such a water parasite as the mistletoe, since it derives water and inorganic salts from the host or stock, while it manufactures its own carbohydrates and proteins. The chief difference between a scion and a parasite is that the former is organically united to the stock, while the latter has haustorial processes which ramify through the host tissues; however, there is no sharp delimitation between the phenomena of parasitism and those of grafting, since scions sometimes develop roots in the stock.

The influence of the stock and the scion upon each other. — Many cases are now known in which either the stock or the scion is influenced by the other, so that a part of the original individuality is lost; particularly in evidence is the influence of the stock upon the scion.[1] Such differences may manifest themselves in physiological behavior, as in changed respiration and synthesis, and particularly in reproductive phenomena; or there may be changes in form, in color, or in chemical composition, as when an apple scion grafted on the wild crab bears more acid fruit. The best known changes concern the time of fruiting; a variety of the apple that requires ten or fifteen years to come into bearing from seed may bear in a year or two if a twig from a sapling is grafted on an old stock, while a twig from an old stock grafted on a sapling does not fruit for years. Some late apples ripen earlier when grafted on a stock of an early variety. Certain species of *Citrus* are more productive when grafted on *Citrus trifoliata* than when growing independently. When the morning glory, which is an annual, is grafted on the sweet potato, which is a perennial, the latter develops its characteristic tuberous roots much earlier than otherwise, thus giving an

[1] In spite of the great array of evidence against it, some able investigators still adhere to the theory that stocks and scions maintain the individuality of their respective species; the remarkable changes here recorded are said to represent only such differences as might be obtained by growing the plants in different soils and climates.

excellent illustration of the influence of the scion upon the stock. When the sunflower, which is an annual, is used as a stock for the Jerusalem artichoke, which is a tuberous perennial, the artichoke scion develops aerial tubers and the sunflower stock is characterized by a large development of secondary wood.

Investigators differ as to whether a chemical compound that is characteristic of a given species or variety can pass into a stock or scion of another species or variety, though it is held generally that readily diffusible organic substances may thus migrate, in addition to water and inorganic solutes. For example, in *Abutilon*, albescence may develop in a green-leaved scion on an albescent stock. The migration of such alkaloids as atropin and nicotine from one graft symbiont to the other may now be regarded as demonstrated. For example, atropin may accumulate in the potato or in the tomato when intergrafted with *Atropa* or *Datura*, and nicotine passes from the tobacco plant (*Nicotiana tabacum*) into *Nicotiana alata* and also into the potato. In all of these cases the alkaloids migrate into the other symbiont, whether the alkaloid-producing species is used as stock or as scion. However, attempts to induce the migration of hydrocyanic glucosid between stock and scion in *Phaseolus* have met with no success. In a number of cases the form of a plant may be changed by grafting, the pear, for example, becoming dwarfed when grafted on the quince; some varieties of the apple, when used as scions, exhibit changes in the compactness of their branching. In the grape, grafting has been found to cause the modification of many characters, such as the size of the vine, the form of the leaf, the size of the seeds and of the fruits, and the juiciness of the fruits. French vineyards have been saved from the ravages of the destructive plant-louse, *Phylloxera*, by grafting the vines on immune American stocks.

Graft hybrids and chimeras. — It has often been supposed that the stock and scion sometimes fuse in such a way as to produce new shoots that are intermediate between the two graft symbionts; such new forms have been termed *graft hybrids*. Famous cases of supposed graft hybrids are: the Bizzaria orange, which is thought to have arisen from a graft of *Citrus aurantium* and *C. medica; Cytisus adami*, which is thought to have arisen from a scion of *C. purpureus* on *C. laburnum;* and *Crataegomespilus*, which is supposed to be a graft hybrid between *Crataegus monogyna* and *Mespilus germanica*. A case has been reported where there arose shoots of intermediate character

when a pear scion was grafted on a quince stock. Usually seedlings from these "graft hybrids" revert to one or the other of the two parent forms, but in at least one instance, progeny of intermediate character has been reported; for example, if white beets are grafted on red beets, about a fourth of the progeny of the white scion is red or reddish. A remarkable fusion of the stock and the scion has been produced by a graft between the tomato (*Solanum lycopersicum*) and the nightshade (*S. nigrum*) in which a bud developed where the two calluses fused, growing subsequently into a shoot that combined the characters of both stock and scion; to the new form thus produced there was given the name *Solanum tubingense*. Several such forms have developed, some of which are nearly intermediate between the parent species, while others more closely resemble either the nightshade or the tomato. Seedlings revert to one or the other of the parent forms. Shoots sometimes arise in which a part is like the nightshade and a part like the tomato; such forms have been termed *chimeras*.

Much difference of opinion has arisen concerning the interpretation of these striking results. One theory is that the new productions (such as *Solanum tubingense*), which are not obvious chimeras, none the less resemble the latter in maintaining the individuality of the two components, the portions of each being aggregated into a sort of patchwork or mosaic; the new forms from this viewpoint are regarded as *hyperchimeras*. Another theory has resulted from a study of forms of *Pelargonium* with white margined leaves, in which it has been found that one of the graft symbionts may serve as a sort of mantle for the other; the body of the new form is composed entirely of one variety, while the epidermis alone, or the epidermis with the hypodermis, is composed entirely of the other variety. These remarkable forms have been termed *periclinal chimeras*. Already it has been shown that *Cytisus adami* is a periclinal chimera, the body being composed of *C. laburnum* and the epidermis of *C. purpureus*. There is reason to believe that *Crataegomespilus* is to be explained similarly. In all of these cases, as in *Solanum tubingense*, a seedling gives rise not to an intermediate form but to a form like one of the parent symbionts. While most of the supposed graft hybrids thus appear to be periclinal chimeras, there are some investigators who still hold to the reality of graft hybrids; in the last analysis a graft hybrid should differ from all kinds of chimeras in the merging of the protoplasm of the two graft symbionts. Such merging has not as yet been demonstrated.

Galls. — *The influence of parasites upon their hosts.* — When a parasite attacks another organism, the activities of the latter may be accelerated or diminished. For example, respiration and transpiration commonly are increased and synthesis commonly is decreased. Para-

sites often secrete deleterious substances which, like many poisons, at first excite various activities, while an increase of these substances causes depression and even local or general death. In other cases the injury caused by parasites consists chiefly in the removal of foods and

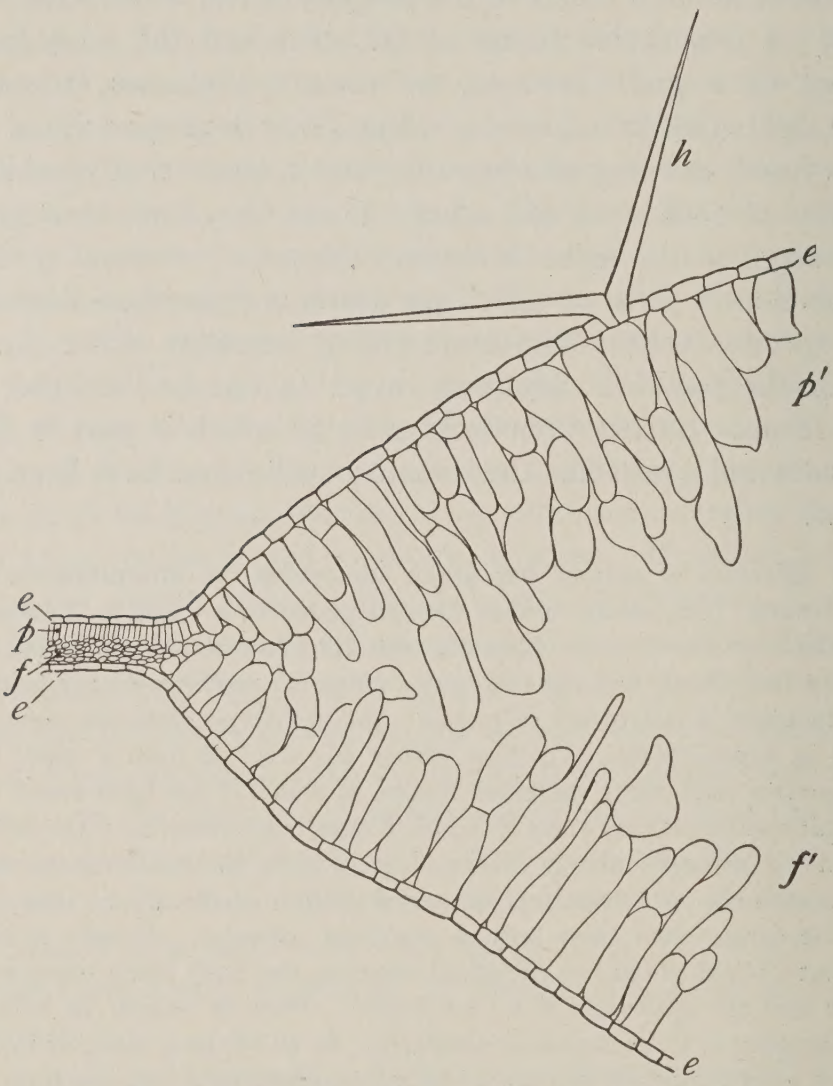


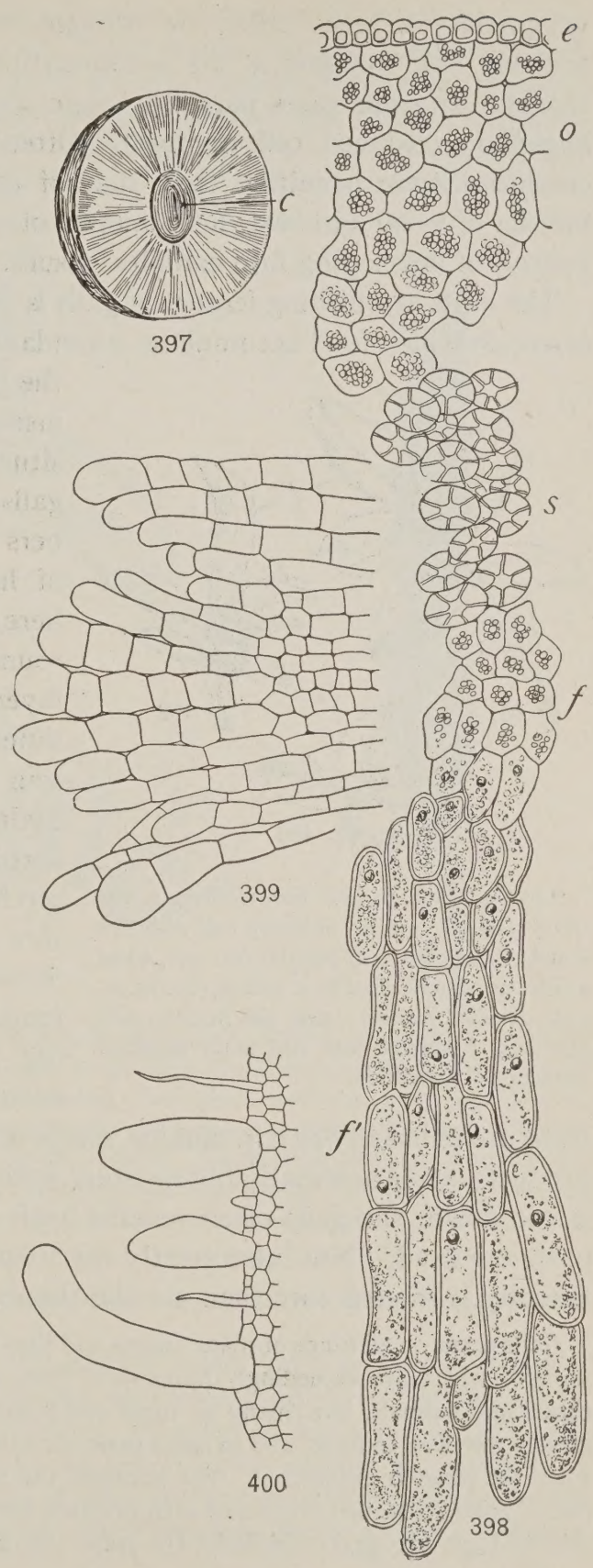
FIG. 396. — A cross section through the edge of a leaf gall of *Viburnum lantana* showing striking hyperplasy and hypertrophy; *p*, the palisade cells of the uninfected portion; *p'* the corresponding cells of the infected portion; *f*, the sponge cells of the uninfected portion; *f'*, the corresponding cells of the infected portion; *e*, epidermis; *h*, epidermal hair; considerably magnified. — From KÜSTER.

food materials from the host, which may in consequence be starved and depauperate.

Various characteristics of galls. — The most conspicuous influence of parasites on hosts is in connection with gall formation. A *gall* is a structural modification of a tissue or of an organ due to another organ-

ism.[1] Commonly the affected tissue is much enlarged, either through *hypertrophy* (cell enlargement) or *hyperplasy* (de-

[1] Galls also are termed *cecidia* and have been contrasted with *domatia*, which differ in that the organisms inhabiting them are thought to be harmless or even beneficial rather than detrimental to their hosts. An example of domatia is afforded by the root tubercles of clover; sometimes the structures inhabited by plant lice are regarded as domatia, since the nitrogenous animal excreta are thought to benefit the plant. It seems wiser to call all such structures galls, regardless of their benefit or harm to the host plant.



FIGS. 397–400. — Cross sections of galls, showing anatomical features; 397, a solid cynipid gall from an oak twig, cut in half; note the radiating lines of tissue, and the central larval chamber (*c*); 398, a section of an oak gall; *e*, epidermis; *o*, cortex, the grains representing plastids (chloroplasts above and leucoplasts with prominent starch grains below); *s*, protective layer of sclerenchymatous cells; *f*, *f'*, nutritive layers adjoining the larval chamber, *f* being a layer rich in starch, and *f'* a layer whose cells are rich in proteins and prominently nucleated; 399, part of the nutritive tissue of the gall of *Nematus gallorum;* note the resemblance to the tissues in an intumescence; 400, isolated nutritive hairs of a Cephaloneon gall from a maple (*Acer*); 398–400, highly magnified. — 397 after KERNER, 398 after LACAZE-DUTHIERS, 399, 400 after KÜSTER.

velopment of new cells), or through both combined (fig. 396). Scarcely less common is the accumulation of food in the affected tissues. In some cases parasites cause *atrophy* (reduced cell size) or *hypoplasy* (reduced cell number). Often gall tissues remain in a condition more primitive than that of uninfected tissues; the primordia of wood and bast, for example, often remain parenchymatous instead of developing into complex tissues.

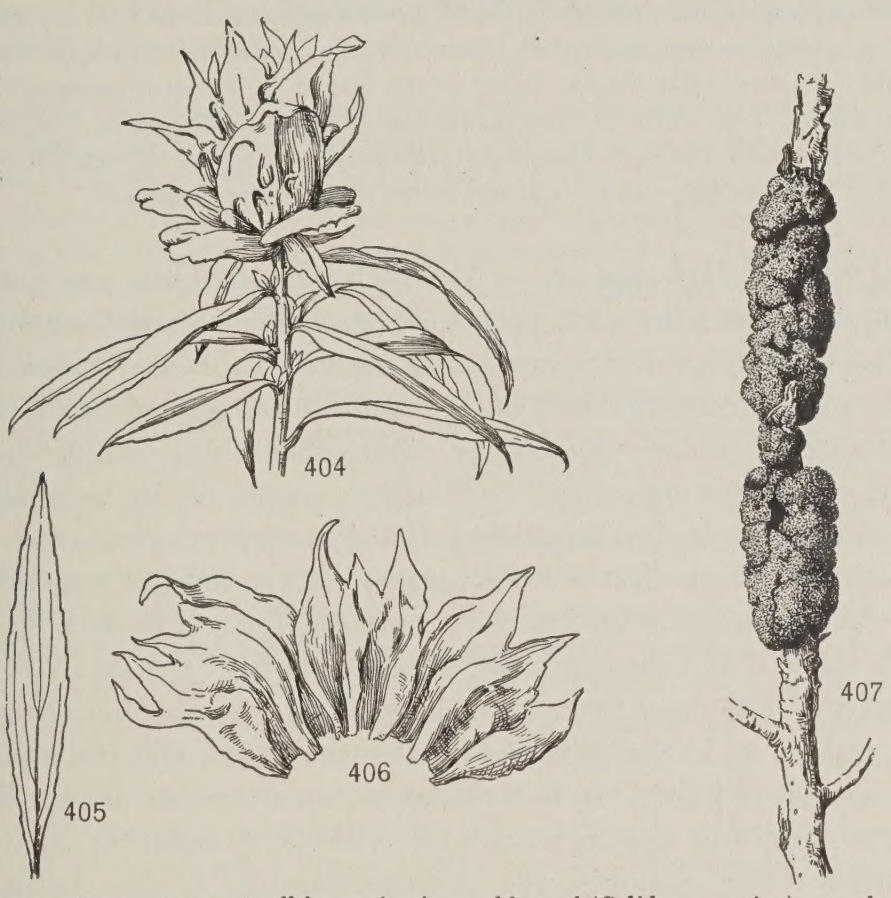
The most astonishing feature of galls is the development of *nutritive layers*, in which food accumulates abundantly, and later is utilized by the parasite, whether fungus or insect. A somewhat complex situation is found in the cynipid galls (*i.e.* galls formed by members of the Cynipidae, a group of highly specialized insects); here the larval chamber is surrounded by well-defined food layers, which sometimes are differentiated into an inner protein layer and an outer carbohydrate layer, the whole being surrounded by a layer of rigid mechanical cells or of protective cork cells (figs. 397–400). Sometimes the nutritive layers remain meristematic, continuing to regenerate as they are destroyed by the insect larvae.

FIGS. 401–403. — Gall formation in a rose (*Rosa blanda*): 401, an ordinary leaf with five leaflets (*l*) and a pair of stipules (*s*); 402, a leaf which has been attackd by a gall-producing insect (*Rhodites bicolor*); note the prickly galls (*g*); 403, a similar leaf still more modified through gall formation.

Galls are unusually rich in tannins, resinous secretions, and other waste products, and are remarkably resistant structures; if an infested plant is cut down, the galls often remain fresh and green when the other parts are dead. Not infrequently the tissues of galls are much more xerophytic in structure than are the tissues of uninfected organs.

Galls occur on all kinds of plant organs and they assume a wide variety of forms, some of which are exceedingly fantastic. They are caused by many species of plants and animals, but chiefly by fungi and insects. Often the organ affected is greatly modified in form, and in some cases structures appear that are not present when the plant is uninfected. For example, the rose gall, formed by the cynipid insect, *Rhodites bicolor*, is covered with prickles, even if the rest of the plant is quite smooth (figs. 401–403); similarly, the grape-vine gall formed by *Cecidomyia vitis-*

pomum (fig. 129), and some cynipid oak galls are pubescent, though the organs concerned are smooth when uninfected. In the common oak gall, formed by *Amphibolips inanis*, delicate threads connect the larval chamber with the gall periphery. Some gall-forming organisms injure the growing point, thus checking elongation, and causing the close imbrication of the developing leaves as in the conelike willow gall formed by *Cecidomyia strobiloides*, and in the goldenrod gall formed by *C.*



FIGS. 404–407. — 404–406 gall formation in a goldenrod (*Solidago serotina*) 404, the apical portion of a plant that has been attacked by an insect (*Cecidomyia solidaginis*); such galls check stem elongation and prevent flowering; note the variation in leaf form; 405, an ordinary leaf; 406, a gall leaf or leaf-complex made up of a number of coalesced leaves; 407, a "black knot" on a branch of the choke cherry (*Prunus virginiana*), an example of gall formation through fungal influence, the stimulating fungus being *Plowrightia morbosa*; the swollen black mass is known as a stroma, and it contains many fructifications known as perithecia.

solidaginis (figs. 404–406). A great many root galls are formed by nematode worms.

An interesting group of galls are the *witches' brooms*, which are formed on various trees (as the white birch, the hackberry, and various conifers) by *Exoascus* and by other fungi, and by the dwarf mistletoe, *Arceuthobium pusillum*. In these galls many small twigs diverge from the part infected, thus manifesting a resemblance to a broom or brush. In the case of *Exoascus* the mycelium hibernates, so that the fungus recurs season after season. Other important fungus galls are: the black

knot of the cherry (caused by *Plowrightia*, fig. 407); the ergot of rye and other grasses (caused by *Claviceps*), in which black protruding bodies, the sclerotia, replace the grains; the cedar apple of *Juniperus virginiana* (caused by *Gymnosporangium*); and the leaf and flower galls of the Ericaceae (caused by *Exobasidium*). Fungi also occasion root galls in the cabbage and in the alder, and bacteria occasion galls on the roots of leguminous plants (p. 303). Sometimes fungi cause pronounced changes in plant habit. For example, the prostrate herbs, *Euphorbia maculata* and *E. polygonifolia*, become erect when infested with a certain rust; comparable modifications, due to similar causes, occur in the leaves of *Anemone quinquefolia* and *Hepatica acutiloba*. Parasitic seed plants less commonly cause galls, though *Conopholis* occasions conspicuous enlargements on oak roots, and the mistletoe frequently occasions stem swellings and variations in the form of the branches.

The cause of gall formation. — Although galls obviously are caused by foreign organisms, the exact nature of the stimuli involved is unknown, and can scarcely be determined precisely until galls are produced artificially under controlled conditions. Some investigators regard chemical stimulation as the ruling factor, while others think that mechanical irritation is more important; still others appeal to the possibility of osmotic changes, a view suggesting analogies with tuberization. Some investigators think that a brief contact with a foreign structure (as with the ovipositor of an insect) is sufficient for gall formation, while others think that long-continued stimulation (as by insect larvae) is necessary. The most remarkable galls are those in which new structures appear, as in the galls of the rose, the grape, and the oak, with their prickles or hairs. In some cases, as in various so-called domatia, gall-like structures appear to develop without stimulation by foreign organisms. For example, the myrmecophytes, *Hydnophytum* and *Myrmecodia*, have large tubers permeated with air chambers and passages that are inhabited by ants, but it has been shown that the chambered tubers develop independently of ant stimulation. It has been discovered that some witches' brooms (as in the spruce) can be propagated by seed, many of the progeny from such shoots being dwarf and bushy. There has been advanced the somewhat dubious theory that structures of this sort once were due to the stimulation of the foreign organism, but that now gall formation has become an inherent feature of the plant.

The advantages of galls. — Unlike most plant structures, galls are obviously disadvantageous to the plants of which they form a part. The energy and material used in their construction, the food which they accumulate and which is utilized by the foreign organism, together

with many activities of the parasites are features of positive detriment. Thus galls furnish one of the best illustrations of the fallacy of the theory of adaptation. In a few cases galls are believed to be advantageous to the host as well as to the parasite, notably in the root tubercles of the legumes (p. 305); if the fungus theory of tuberization is confirmed, there becomes evident another striking case of gain through gall formation.

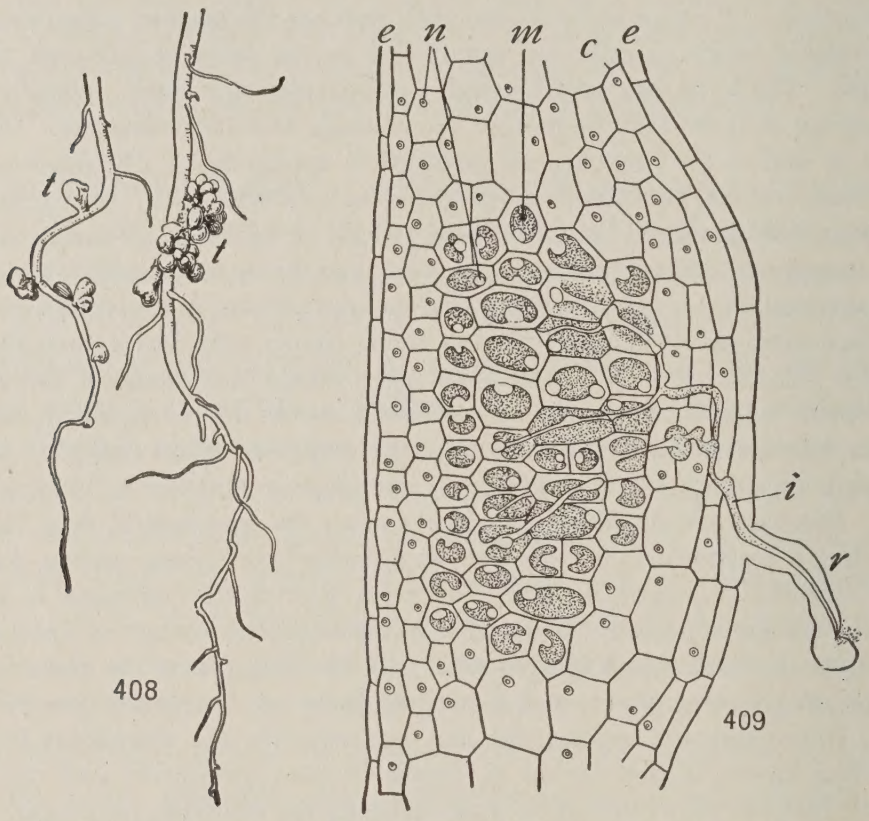
Fasciation. — Perhaps to be classed with galls are the peculiar structures known as *fasciations*, which usually are manifested in the form of flattened stems or branches. The form may arise through the flattening of a single cylindrical stem, or a number of stems may be merged into a single fasciated structure. Often the flowers as well as the branches are modified in appearance. The phenomenon is not well understood, but often it is believed to be associated with " over-nutrition "; sometimes it is produced by mechanical causes, or by insect or fungal activities (as in *Oenothera*). Fasciation sometimes appears to be inheritable, as in *Celosia*.

Autoparasitism. — *Autoparasitism* (*i.e.* self-parasitism) is a common phenomenon, since most plants contain colorless living tissues that derive their food from the green chlorenchyma. In some cases green plants bear albescent shoots whose nourishment is parasitic; in the redwood such shoots occur frequently, and when they are detached and planted in the soil, they may develop chlorophyll. In plants possessing an alternation of generations, one phase commonly is parasitic on the other. For example, in liverworts and mosses the sporophyte foot (an organ resembling a haustorium) is embedded in gametophyte tissues, and in *Anthoceros* it has rhizoid-like processes; since the moss sporophyte commonly is green, it probably is a water parasite comparable to the mistletoe, though in *Sphagnum* the sporophyte is colorless and holoparasitic. In the seed plants the gametophyte is parasitic on the sporophyte, and sometimes there are haustorial processes, as in *Zamia;* the embryonic sporophytes also are parasitic, the suspensors frequently resembling haustoria and acting as organs of food absorption and conduction. Parasitic features are exhibited by many germinating seedlings, particularly among the monocotyls, in which the tip of the cotyledon often is a haustorial organ (figs. 536, 537) and secretes digestive enzymes. Grass seedlings have a peculiar organ, the *scutellum*, which connects the embryo with the region of accumulated foods; often the scutellum cells are elongated, in *Briza* even resembling root hairs. Perhaps to be noted under autoparasitism is the occasional parasitism of a dodder plant upon another dodder, of mistletoe upon mistletoe, or of strong individuals upon weak individuals among the Euphrasieae.

3. RECIPROCAL PARASITISM, HELOTISM, AND ENDOSAPROPHYTISM

Definitions. — The topic symbiosis commonly has been subdivided into antagonistic symbiosis or parasitism and coöperative symbiosis or mutualism. Such terms as mutualism and coöperation are humanistic,

and should be discarded. Each of two symbionts may be benefited nutritively or otherwise by the presence of the other, but it is a misconception to regard two symbionts as giving one another food or assistance. That form of symbiosis in which each of the symbionts obtains food from the other may be termed *reciprocal parasitism;* where the parasitism of the two symbionts is alternative rather than simultaneous, the relationship may be called one of *alternative parasitism.* The



FIGS. 408, 409. — 408, roots of the white sweet clover (*Melilotus alba*), showing the characteristic root tubercles (*t*), which are induced by a special bacterial form, *Bacillus radicicola;* note the grouping of tubercles in clusters; 409, longitudinal section through a part of a root of the pea (*Pisum sativum*) that has begun to tuberize by reason of the stimulating influence of *Bacillus radicicola;* invasion occurs through the root hairs (*r*), where infection threads (*i*) are formed, these penetrate the cortical tissues (*c*), where branching takes place; note that the infected cortical cells have denser cytoplasm, larger nuclei (*n*), and thicker walls than the uninfected cells; *e*, epidermis; highly magnified. — From FRANK.

term *helotism* (*i.e.* slavery) may be employed in cases where one symbiont derives appreciable nutritive benefit without conspicuous gain or loss to the other. Thus helotism is intermediate between parasitism, where one symbiont gains and the other loses, and commensalism, where parasitism is absent. Where one symbiont lives

within another, obtaining food saprophytically rather than parasitically, it is said to exhibit *endosaprophytism.*

Root tubercles and their bacteria. — *Structure and behavior.* — Reciprocal parasitism is best illustrated by the relation existing between the Leguminosae and the bacteria which inhabit galls on their roots; these galls are caused either directly or indirectly by the bacteria and are known as root tubercles (fig. 408). The tubercles, like most galls, are composed chiefly of large parenchymatous cells, many of which, especially in the central region, contain bacteria belonging to the species *Bacillus* (or *Pseudomonas*) *radicicola* (fig. 409). These bacteria are facultative forms that are present somewhat generally in the soil as saprophytes, appearing usually as minute motile rods. They enter the roots of leguminous plants through the root hairs, exhibiting prochemotactic reactions to certain root excretions, and appearing to secrete substances which soften or dissolve the walls of the root cells. Soon after the bacteria thus become parasitic, there appear hypha-like *infection threads* or *bacterial tubes*, which are essentially gelatinous masses of minute bacteria known as *zoögloea.* The bacteria in these zoögloea masses bud like yeast, giving rise to motile or immotile rod-like forms, which in turn produce the peculiar branched forms, known as *bacteroids*,[1] that are characteristic of the tubercles. Finally, the organisms become dissolved and incorporated into the body of the green plant. Tubercle formation is associated definitely with bacterial infection, and starch may accumulate in the hypertrophied cells as in other galls.

While the root bacteria of the Leguminosae commonly are referred to a single morphological species, there are several and perhaps many well-defined physiological species. Commonly it is easy to infect the root of a legume with bacteria from a legume of the same species or even genus, but usually it is difficult or impossible to do this if the bacteria are taken from another genus; however, peas are infected readily by bacteria from vetches, and vetches may be infected similarly from peas. Bacteria from the roots of peas thrive only moderately in the roots of beans, but if these bacteria are used to inoculate other bean roots, they grow as vigorously as did their immediate ancestors in the roots of peas. Similarly, bacteria from legumes of calcareous soil do not infect legumes of siliceous soil, nor *vice versa*, but if the acid content of a calcareous soil is increased slowly, a race of bacteria can be developed (*e.g.* on alfalfa) that eventually will be able to infect lupines growing in siliceous soil. It is the belief of bacteriologists that through similar progressive

[1] This name dates back to the time when the organisms were regarded as an albuminous product of the green plant. The term *Rhizobium* was given to these bodies when they were supposed to be organisms, but of unknown affinity.

variability any race of *Bacillus radicicola* can be grown eventually on any legume root, and this view is favored by the fact that when a leguminous crop is introduced into an entirely new region, the roots soon become infected by bacteria which induce tubercle formation. The bacteria of legume tubercles thrive only where free nitrogen and an abundant supply of carbohydrates are available, their development being retarded by an abundance of nitrates. Similarly, the tubercles reach their best development in soils that are poor in nitrates; they vary from the size of a pinhead in ordinary clovers to the size of a pea in *Strophostyles helvola*, a plant of sandy beaches. The tubercles live but a single season, hence in perennial legumes there is a new bacterial infection each year.

Nitrogen fixation and nitrification. — Although it is an abundant and important constituent of plants, only a comparatively small number of plants, namely, certain bacteria and fungi, are known to be able to utilize directly the free nitrogen that exists so abundantly in the air. This incorporation of free nitrogen into nitrogenous compounds within the body is known as *nitrogen fixation*, and it is a process of vast importance to the entire organic world. The first organism definitely ascertained to have the power of nitrogen fixation was *Clostridium pasteurianum*, one of the anaerobic soil bacteria. A number of nitrogen-fixing organisms are now known, embracing various widely distributed species of *Azotobacter* (a genus of aerobic bacteria) and of *Bacillus*, such as *B. radicicola*, the organism inhabiting legume tubercles, and *B. amylobacter*, which is thought by some investigators to include forms that have been referred to *Granulobacter* and *Clostridium*.

Probably the most important of all nitrogen-fixing organisms is *Azotobacter chroococcum*, which in temperate climates is abundant in nearly all soils and also in fresh and salt water, being absent chiefly in bogs and in some virgin soils. Nitrogen fixation by this organism is best accomplished in aerated soils and is facilitated by lime and phosphorus and retarded by acids. Contrary to earlier views, humus facilitates nitrogen fixation by *Azotobacter*, probably because of its microörganisms; it has been suggested, for example, that cellulose-destroying bacteria furnish carbohydrates in available form for nitrifying organisms, and it has been shown that the addition of sugar to cultures facilitates nitrogen fixation. In addition to the bacteria, some yeasts and a number of fungi are now thought to be able to fix free nitrogen (p. 312). Some investigators have claimed that the hairs of many plants are able to fix nitrogen; the fact that the amount of nitrogenous materials in such hairs is inconsiderable and that this small amount is no less when the hairs develop in an atmosphere devoid of nitrogen make the claim very doubtful. At the same time it must be admitted that the known methods of nitrogen fixation seem inadequate to account quantitatively for the large and relatively constant supply of available nitrogen in the soil, particularly in view of the considerable amount of denitrification that is effected through the activity of various bacteria.

In the processes of organic decay the complex proteins are broken up into simpler substances, such as organic acids, amines, and ammonia. Some of these, as ammonia, are oxidized through the agency of bacteria, constituting a process that is known as *nitrification*. The first step in this process is the formation of nitrites, and from these by further oxidation are formed nitrates. Different organisms are concerned in the two stages, *Nitrosomonas*, for example, oxidizing ammonia into nitrites, and *Nitrobacter* oxidizing the latter into nitrates. The nitrates formed by this process are utilized readily as a source of nitrogen by most plants.

Green plants on the one hand and nitrogen-fixing and nitrifying bacteria on the other have a reciprocal relation of vast significance, for the former produce carbohydrates and the latter nitrates, each of which is of great importance for the other, as well as for all living organisms. Thus there is a sort of universal symbiosis between the carbohydrate-forming and the nitrate-forming organisms. The origin of this symbiosis is unknown, but it is possible that the first plants were able to fix nitrogen as well as to manufacture carbohydrates, and that divergent evolution has since taken place. Even among plants now living there are some bacteria, notably *Nitrosomonas* and *Nitrobacter*, which can manufacture carbohydrates as well as nitrites or nitrates. Sometimes nitrate-forming and carbohydrate-forming organisms are in somewhat close symbiosis, as in the case of *Azotobacter* and *Oscillatoria*, or *Azotobacter* and *Nostoc*, which are two of many similar associations, where both symbionts grow with unusual vigor; similarly, in salt water, *Azotobacter* lives in luxuriance in the mucilage which coats the fronds of *Laminaria*. In all of these cases the amount of nitrogen fixation is greatly beyond the usual, whence it has been urged that algae can fix nitrogen, though it seems more likely that such symbiosis stimulates the bacteria to larger activity because of the carbohydrates which the algae manufacture. An interesting but poorly understood case of symbiosis is that which exists between bacteria and myxomycetes, two groups of organisms that often are closely associated; it is claimed, even, that the spores of some myxomycetes, for example, *Dictyostelium mucoroides*, fail to germinate except in the presence of bacteria, and that the food of myxomycetes consists largely of such microörganisms.

The rôle of bacteria in legume tubercles. — It has been known for centuries that leguminous plants enrich the land when their roots are left in the soil; furthermore, the high nitrogen content of the root tubercles

was known long before the tubercle bacteria or their power of nitrogen fixation was discovered. Hence it is not strange that once the tubercles were regarded as organs which manufacture or accumulate protein. Even before it was empirically proven that *Bacillus radicicola* fixes free atmospheric nitrogen, a comparable conclusion was reached by elimination, for it was shown that nitrogenous compounds do not develop in sterilized soils, and that the legumes, unlike other plants, thrive in soils devoid of nitrogenous compounds; moreover, tubercles do not develop and the plants are depauperate if the soil is sterilized.

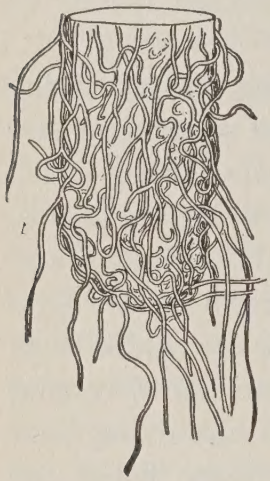
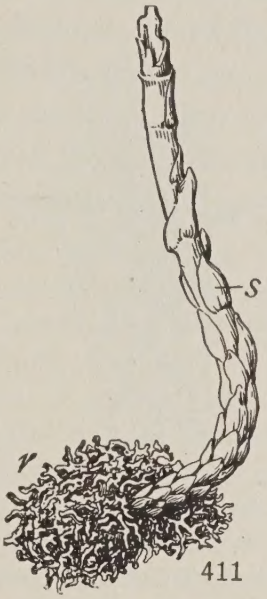


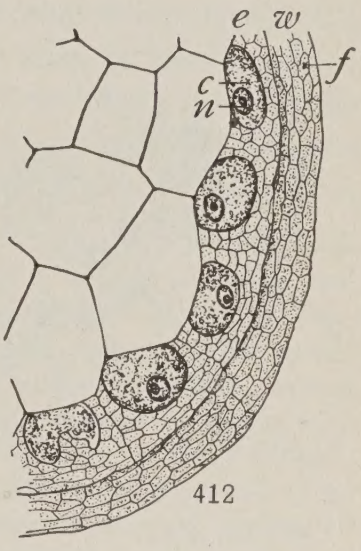
FIG. 410. — A root tip of the European beech (*Fagus sylvatica*), illustrating ectotrophic mycorhiza; the fungal hyphae (*h*) form a dense layer which ensheathes the root; considerably magnified. — After FRANK.

There is now ample direct evidence that *Bacillus radicicola* can fix free atmospheric nitrogen to some extent when isolated in pure cultures, and much more abundantly when growing in the roots of leguminous plants, the resulting compounds accumulating within the bacterial body. Such nitrogen fixation has been shown to be facilitated by the presence of an abundance of sugar, especially maltose, and of free nitrogen, and to be etarded by the presence of an abundance of nitrates or of albuminous substances. It is scarcely to be doubted that *Bacillus radicicola* and the leguminous plants live in a state of reciprocal parasitism, the bacteria deriving carbohydrates from the legumes, while the latter derive nitrogenous compounds from the bacteria. The parasitism of the two symbionts appears in part alternative. The bacteria soon after entrance into the root exhibit great vigor and activity, probably through their bettered food relations, while the legume is injured rather than benefited by their presence, since in the cells which they occupy the bacteria utilize the starch and much of the cytoplasm and cause the nuclei to become partly disorganized. After a time the leguminous plant appears to overcome the bacteria, and it enters upon a state of vigor because of the appropriation of nitrogenous compounds, while the bacteria enter the bacteroid or *Rhizobium* state of relative inertness, after which there is no recovery of the power to fix nitrogen or to infect other leguminous roots; probably some nitrogenous compounds become available for the legume during the later phases of

bacterial activity, though it is through the final dissolution of the bacteroids that the main supply appears to be derived.

Mycosymbiosis. — *Ectotrophic and endotrophic mycorhiza.* — Fungi are associated habitually with the roots of many plants, such as the oaks, pines, orchids, and ericads (Ericaceae). The root in combination with its fungus is known as a *mycorhiza* (*i.e.* fungus root), and the phenomenon may be termed *mycosymbiosis*. If the fungal hyphae invest the roots, as in the beech (fig. 410), the mycorhiza is called *ectotrophic* (*i.e.* nourished outside), while if the fungi occur within the roots, as in the orchids (fig. 413), it is called *endotrophic* (*i.e.* nourished within).

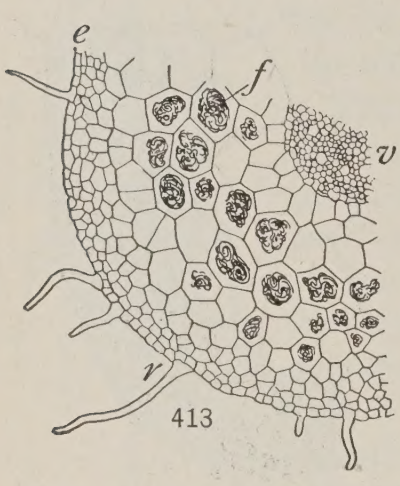




FIGS. 411, 412. — Mycorhiza of the Indian pipe (*Monotropa uniflora*): 411, the basal portion of a stem with its clump of roots; note the coralloid root system (*r*), and the imbricated scale leaves (*s*); 412, a cross section through the outer part of one of the coralloid roots, showing the compact arrangement of the fungal hyphae which form a pseudo-parenchyma (*f*); note that the fungus is partly ectotrophic and partly endotrophic, the hyphae penetrating into the epidermis (*e*) of the root and crowding aside the cytoplasm (*c*) of the latter; *n*, the nuclei of the epidermal cells; 412 highly magnified.

A modified form of the latter has been recognized in which the fungal hyphae do not penetrate the cells of the root, but invade the cortex as well as the epidermis of the roots. Such mycorhizas have been termed *ectendotrophic*. It is also evident that the distinction between ectotrophic and endotrophic mycorhizas is by no means as sharp as it was formerly thought. Intermediate forms exist. With few exceptions the ectotrophic (including the ectendotrophic) mycorhizas are limited to woodland soils and are there associated with trees and shrubs. They vary from forms with loose and scattered hyphal threads which come into casual and temporary contact with the roots to a permanent condition like that in *Monotropa*, where the root system usually is compacted into a clump or ball and where the individual rootlets are so closely in-

vested by fungal hyphae that the latter, when sectioned, resemble a compact tissue (figs. 411, 412). In such a case the root proper does not come into contact with the soil. The hyphae composing the fungal root sheath connect with the mycelia that permeate the humus. The rootlets of the beech and of most plants with prominent ectotrophic mycorhizas are relatively short and thick and have a coralloid aspect; moreover, growth is relatively sluggish, and root hairs are few or wanting except on roots or on parts of roots that are comparatively free from fungi.



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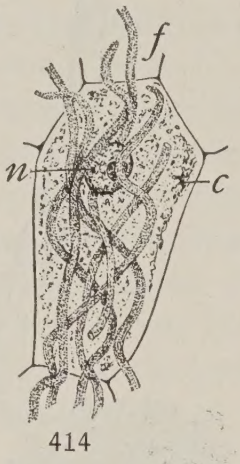

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FIGS. 413, 414. — Endotrophic mycorhiza of orchid roots: 413, a cross section through a part of a root of *Aplectrum hyemale*, showing dense clumps of fungal hyphae (*f*) in some of the larger cortical cells, several rows inside of the epidermis (*e*); *r*, root hairs; *v*, vascular tract; 414, a single cortical cell from the root of *Spiranthes cernua*, showing fungal strands (*f*), cytoplasm (*c*), and the nucleus (*n*); 413 considerably, and 414 highly magnified.

Ectotrophic mycorhizas have been found on various kinds of trees and shrubs, being especially well developed on such forms as the beech, birch, aspen, pine, spruce, and larch. In many instances the fungi have been isolated, grown in pure cultures, and new mycorhizas have been formed by applying the fungi from the cultures to sterile roots. Many such fungi have been identified and shown to be species of common woodland mushrooms so that there is now a long list of fungi known to produce mycorhizas on tree roots. Various species of *Boletus* appear to be among the most frequent of the mycorhizal fungi, but the list also includes such common genera as *Amanita*, *Russula*, *Lactarius*, *Cortinarius*, and *Tricholoma*. In addition to such mycorhiza formers, fungi referred to the genus *Rhizoctonia* have been isolated from the roots of young pines. Here the relationship seems to be purely parasitic and the infested roots have been termed *pseudomycorhizas*.

Endotrophic mycorhizas, which especially characterize the orchids and the ericads, are in many respects much more specialized than are the ectotrophic forms. Orchid roots are characteristically fleshy and

tuber-like, differing much more from ordinary roots than do those associated with ectotrophic fungi; furthermore, the endophytic fungi appear to be specialized forms rather than ordinary soil fungi. Certain cortical cells contain closely interwoven clumps of hyphae which commonly enfold the nucleus, and there are hyphal connections with similar clumps in adjoining cells, so that the mycelium often is continuous (figs. 413, 414); frequently also haustoria are present, and sometimes the internal hyphae are continuous with the hyphae which ramify the soil. Root hairs commonly are scarce and are more or less filled with hyphae. Many root cells are free from fungi, including some of the outer cells as well as those of the vascular tract.[1] The fungi of orchid mycorhizas have usually been referred to various species of *Rhizoctonia*.

The heaths have been shown to abound in endotrophic mycorhizas which have been most carefully investigated in the common heather (*Calluna vulgaris*). In contrast with the orchids the heather has extremely fine roots consisting of a slender vascular strand surrounded by a single layer of large cortical cells. Under ordinary conditions of growth every cortical cell encloses a mass of densely branching mycelium which is continuous with the hyphae on the external surface of the root. The fungus does not seem to penetrate the vascular cylinder. Throughout the growing season the mycorhizal cells exhibit active digestion of the mycelium. This fungus, moreover, is not confined to the roots but also invades all the tissues of the shoot with excessively fine hyphae which are usually confined to the middle lamella of the cell walls. In the organs of the flower the mycelium is relatively abundant and the testa of the seeds carries it over to infect the roots of the germinating seedlings. Similar endotrophic mycorhizas have been shown to be present in various blueberries (*Vaccinium*) with similar infection of the seed coat providing for the transmission of the endophyte to the roots of the seedlings. The mycelium has been isolated from young roots, from shoots, and from seeds and used to inoculate seedlings free from infection where it reproduces mycorhizas. The endophyte has been identified as *Phoma radicis*. Similar mycorhizas have been found in many other members of the heath family and it seems probable that nearly all the Ericaceae possess them.

Endotrophic fungi have been found to be commonly present in the fleshy, sparingly branched roots of *Ophioglossum*, in the roots of Marattiaceae, and in the roots of many members of the Osmundaceae and Polypodiaceae. Similar endophytic fungi are also present in the prothallia of most of these ferns, in the tuber-like gametophytes of *Lycopodium* and *Botrychium*, and in many of the liverworts.

The prevalence of mycosymbiosis. — Formerly mycosymbiosis was believed to be a somewhat rare phenomenon, characterizing only a

[1] In *Corallorhiza*, which has no roots, fungi occur in the rhizome and in its "root hairs," and in *Aplectrum*, which has ordinary endophytic root fungi, the removal of the corm is followed by the development of coralloid rhizomes that bear "root hairs" and contain fungi, precisely as in *Corallorhiza*.

few families, such as the conifers, ericads, orchids, and oaks; but now it is believed that a majority of ordinary green plants are *mycophytes* (*i.e.* fungus plants), as green plants with root fungi may be called. In Germany seventy out of a hundred and five species taken at random had root fungi, and in Java sixty-nine out of seventy-five. In a deciduous forest in Illinois with 145 species in 114 genera mycorhizal fungi were found in 93 species distributed among 76 genera. Doubtless the ectotrophic fungi are more abundant than the endotrophic, though the latter occur in numerous forms, as in aroids, lilies, and many ferns, as well as in orchids and ericads; it is probable also that many of the former are mere contact forms without particular significance. Endotrophic fungi are now well known in some mosses (as *Buxbaumia* and *Tetraplodon*) and in many liverworts (notably in the Jungermanniales, but also in *Fegatella* and *Marchantia*). Mycorhizas with characteristic coralloid rootlets and hyphal clumps have been detected in certain Carboniferous plants, as in *Cordaites*, thus attesting to the antiquity of mycosymbiosis. For the most part root fungi are absent in sedges, pinks, crucifers, and legumes, though the last are characterized by bacterial symbiosis. As might be expected, mycorhizas are associated abundantly with plants rooted in forest mold. They are rare in water and in wet soils (except in bogs) and are almost universal in bulbous and tuberous plants.

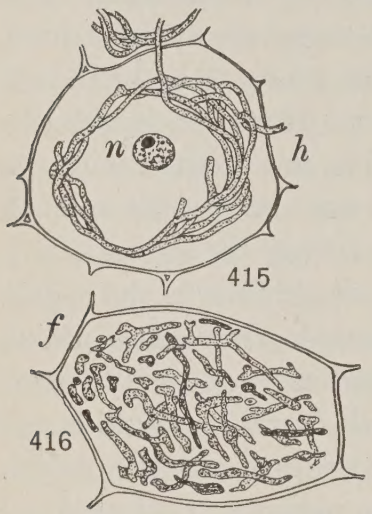
The rôle of root fungi. — While root fungi have long been known, it originally was supposed that their contact with roots is merely casual, or that they represent ordinary parasites. It is now known that there are all conditions of relationship between the root fungi and their hosts, ranging from casual and temporary association, apparently of little importance to either the fungus or the host, to obligate symbiosis and harmful parasitism. In many trees the mycorhizas are produced during the summer and autumn, persist during the winter, and die in the spring. These mycorhizas seem of little importance to the trees, especially as comparatively few rootlets are affected. Some years since it was suggested that *Monotropa* is likely to have a nutritive relation with its fungus, since the latter completely invests the root system. Careful experiments on beech seedlings demonstrated that while the plants developed vigorously in ordinary soil, ten out of fifteen seedlings grown in sterilized soil died within two years, in spite of a greater than usual development of root hairs. Experiments with pine seedlings resulted similarly, although no difference appeared between the cultures

the first year. In contrast to these results it was claimed that species without root fungi grow more luxuriantly in sterilized than in ordinary soil; it should be said, however, that some investigators regard this last experiment as inconclusive. In general it seems that mycorhizal fungi facilitate the intake by the trees of ammonium salts and other organic compounds of nitrogen present in the humus.

It has been demonstrated that orchids are dependent upon their symbiotic fungi to a surprising degree. As a group, orchids have been regarded as difficult of cultivation, and for a long time their seeds were supposed to be incapable of germination. However, it was discovered that the thing requisite for germination was contact with the appropriate fungus, in which respect orchids are comparable to such holoparasites as *Orobanche*. Of great interest from the evolutionary standpoint is the fact that various species of orchids differ in the degree of their dependence upon their fungi. For example, the seeds of *Bletia* germinate without fungus contact, and the seedlings continue to grow as autophytes for several months, when growth ceases, never to be resumed, unless the appropriate fungus comes in contact with the orchid. In *Laelia* and *Cattleya* the autophytic seedling period is much shorter, while in *Cypripedium* and *Neottia*, fungus contact is necessary for the initial phase of germination. In nature the fungus almost always enters the young seedling at the outset. When fungi are introduced into cultures of minute orchid seedlings, a synthesis of hitherto separate individuals takes place that is altogether comparable to the formation of lichens through the synthesis of algae and fungi (p. 315). More recently it has been shown that orchid seeds may be germinated and the seedlings grown successfully in pure cultures, without fungi, by the addition of certain sugars to the culture medium. Healthy seedlings of *Cattleya*, *Laelia*, *Cypripedium*, and other orchids were grown thus and after development had reached a certain stage the seedlings were transplanted to a suitable medium containing inorganic salts only. There they continued to grow independently of fungus infection.

The data just given appear to indicate that some mycophytes, at any rate, are parasitic or at least dependent upon their root fungi. There is evidence also of parasitism in the opposite direction. Gall formation, cell hypertrophy, and nuclear disorganization have already been mentioned, and they indicate the probable parasitism of root fungi upon green plants; since these fungi also live as saprophytes in the soil, they appear to belong to the group of facultative parasites. Careful cytolog-

ical study in *Neottia* has shown that in certain cells (fungal host cells, fig. 415) the hyphae have haustoria and are vigorous and healthy, clearly living parasitically on the orchid, while in other cells (digestive cells, fig. 416), the orchid appears to be destroying and digesting the fungal hyphae. Similarly contrasting host cells and digestive cells have been observed also outside of the orchids, as in *Calluna*, *Podocarpus* and *Psilotum*. These are representative instances of reciprocal parasitism, and it is rather likely that similar nutritive relations occur in many other mycorhiza plants, though how widely it is not yet possible to say.



FIGS. 415, 416. — Cells from the root of an orchid (*Neottia nidus-avis*): 415, a fungal host cell in which the hyphae (*h*) are vigorous and apparently parasitic upon the orchid; *n*, nucleus; 416, a digestive cell in which the hyphae are being disorganized and digested by the orchid; highly magnified. — After MAGNUS.

The substances appropriated from one another by the two symbionts are not certainly known, though there is strong presumptive evidence in certain cases that the interrelations in part resemble those existing between leguminous plants and their tubercle bacteria. Careful study in certain forms has shown that starch and other carbohydrates disappear from the root cells coincidently with an obvious increase in the fungal cytoplasm. In some forms there is evidence that food passes from the root to hyphae in the soil, one observer regarding the root tannins as the source of food. On the other hand, it has been observed that the entrance of fungi into a root may be followed by increased activity in the root cells and by nuclear enlargement, and also by a considerable increase in proteins; in *Podocarpus* proteolytic enzymes appear upon fungal entrance. It is now thought that a number of fungi are able to fix nitrogen; among these are such common forms as *Aspergillus* and *Penicillium*. It has been shown that the endotrophic fungus of *Podocarpus* is able to fix nitrogen, and several species of *Phoma* that have been taken from the roots of ericads have been found able to fix nitrogen more economically than *Azotobacter*. Thus it is becoming increasingly likely that root fungi are important sources of nitrogenous compounds for mycophytes. However, experiments on the orchid fungi as yet give negative results,

and it may be that nitrogen fixation is a function of certain root fungi rather than of root fungi in general. Also of interest in this connection is the demonstration of nitrogen fixation by the parasitic fungi that frequently inhabit the aerial organs of *Lolium*, resulting in increased nitrogen content and greater vigor in the latter.

From the foregoing it seems likely that the fungus appropriates carbon compounds from the green plant, while the latter probably appropriates nitrogenous substances from the fungus. It has been suggested also that ectotrophic fungi and even endotrophic fungi may take the place of root hairs as organs of absorption of water and salts; in any event root hairs are scarce in mycophytes. Since fungal hyphae are better absorptive structures than are root hairs, mycophytes may be better off nutritively than autophytes, especially if they are able to utilize the substances absorbed from the soil by their fungi.

In cases of mycosymbiosis where neither symbiont is green (as in *Monotropa* and *Corallorhiza*), the gain to the fungus is less evident and to the larger symbiont more evident than usual. *Monotropa* appears usually to be entirely dependent upon its fungus, since its roots are completely invested; sometimes, however, *Monotropa* has elongated roots without fungal sheaths, a fact which seems to indicate that its nourishment then is derived saprophytically. *Corallorhiza* must also depend upon its fungus, unless it is able to absorb food saprophytically from the humus, a matter that is as yet uncertain.

There have come into prominence two further theories concerning mycosymbiosis. One theory is merely the revival of the old hypothesis that the fungus alone is parasitic; favoring this view is the fact that in the bryophytes fungal symbiosis seems to cause diminished rather than increased luxuriance, and that the endotrophic mycorhizas of various plants (as the olive) is best developed on the weaker rather than on the stronger trees; also it has been observed that the seedlings of oaks and chestnuts have been killed in large numbers when their ectotrophic fungus is more vigorous than usual, and especially when it becomes endotrophic. The latter instances, however, may be explained in line with the prevailing theory as merely a disturbance of the usual balance between the two symbionts. The other theory is that the fungus is a harmless endosaprophyte, living upon such root excreta as tannin or upon such foods as sugar. Supporters of the theory of parasitism and of that of endosaprophytism generally agree that the fungus alone is benefited by the symbiosis, the digestion of the fungus by the root cells being regarded merely as the destruction of a foreign organism, that is, as *phagocytosis*. It is conceivable that all the theories here mentioned are valid, for the possibility must be recognized that in the many cases of mycosymbiosis there is opportunity for fundamental differences in the nutritive relations of the symbionts.

Probably to be compared with the mycorhizas are the fungus-containing root tubercles of *Alnus*, *Shepherdia*, and *Elaeagnus;* as in the Leguminosae, cultures of these plants without tubercles result in depauperate individuals, and there is

supplementary evidence that the fungi are able to fix nitrogen. As in the orchids, the fungi may occur in hyphal clumps and may exhibit various stages of disintegration, thus indicating digestion or phagocytosis by the root cells. One investigator regards the organisms of the alder tubercles as bacteria rather than as filamentous fungi, and he claims to have demonstrated the existence of infection threads, rodlike forms, and bacteroids, as in the tubercles of the Leguminosae; *Myrica* and *Ceanothus* are said to have similar root swellings containing similar organisms. The roots of *Cycas revoluta* have coralloid galls which contain colonies of bacteria, fungi, and blue-green algae. Recent studies appear to demonstrate the existence here of reciprocal parasitism, the host cells showing structural alterations, nuclear degeneration, and the loss of starch, while there also occur clumps of fungal hyphae in various stages of degeneration; after the digestion or phagocytosis of the fungi has taken place, the host cells contain various excretory products. Unlike legume tubercles, cycad and alder tubercles are perennial.

The significance of mycosymbiosis.—The discovery of mycosymbiosis alters previous conceptions concerning the prevalence of autophytism. Apparently, ordinary green plants may be divided into autophytes and mycophytes; the latter also include a few plants without chlorophyll. The former are not only free from root fungi, but they also reach their optimum development in sterilized soil, probably because their root hairs are more imperfect absorptive organs than are fungal hyphae. Contrasted with these are the mycophytes,[1] which attain their optimum development in association with root fungi. Between extreme autophytes such as the crucifers, and obligate mycophytes such as the orchids, there exist all gradations; for example, liverworts such as *Preissia* and *Fegatella* are facultative mycophytes, growing either with or without fungi. Generally in autophytes roots and root hairs are well developed, starch is abundant, transpiration is relatively intense, and growth is rapid, while in obligate mycophytes root development is weak, root hairs are few or wanting, transpiration is slight, and growth is slow.

Even though the total number of mycophytes may surpass that of the autophytes, it is not to be inferred that fungal hyphae surpass root hairs in importance in green plants as a whole, for the majority of mycophytes have root hairs and only a relatively sparse development of root fungi; probably many of these plants are facultative mycophytes in which the fungal relation is relatively casual and is attended

[1] The relation here pictured also has been termed *symbiotic saprophytism*, since the relation of the symbiotic complex to the soil is saprophytic. Most cases of so-called holosaprophytism in the higher plants (such as in *Lycopodium*, *Monotropa*, and *Corallorhiza*) are to be referred to symbiotic saprophytism or mycophytism.

with no particular benefit or injury to either symbiont. But the importance of fungi in the nutrition of the higher plants probably is much greater than generally has been suspected, in spite of the fact that the matter may be one of great economic importance. It is very likely that the well-known difficulty in cultivating many of the Pinaceae, Fagaceae, Orchidaceae, and Ericaceae, as contrasted with the ready cultivation of the Cruciferae and Rosaceae, may be due to the fungal symbiosis of the former; many orchids are now grown successfully by taking care that conditions are made suitable for their fungi. Very probably the ability of many plants (such as the ericads) to flourish in bogs, where nitrogen fixation or nitrification by bacteria is relatively rare, is because they live symbiotically with fungi which are capable of fixing nitrogen. It is common to picture organic life chains leading from such dependent forms as animals or fungi back to green plants, which in the sunlight manufacture foods from inorganic raw materials. A truer picture of the plant kingdom is one that recognizes symbiosis, bringing out the dependence of mycophytes upon their fungi, of legumes upon their bacteria, and of other green plants upon the soil bacteria, as well as the dependence of all of these lower forms upon the green plants.

The origin of mycosymbiosis. — There is no adequate evidence upon which to base speculations concerning the origin of mycorhizal phenomena. Very probably the initial phases resembled those postulated for the origin of parasitism, and chemotropic reactions may well have played an important part; indeed, it has been clearly demonstrated that some root fungi are prochemotropic with respect to certain substances that are within or about roots. Probably fungus contact with roots originally was casual, and the first mycosymbiosis doubtless was facultative; later, it may be supposed, came obligate mycosymbiosis, reaching its culmination in the orchids and ericads, and especially in those species that require fungus contact for germination, and in such forms as *Neottia* and *Monotropa*, which contain no chlorophyll and thus depend entirely upon outside sources for their food. It is to be observed that generally the fungus does not become thus dependent upon the other symbiont, but remains facultative, although there is evidence of considerable dependence upon specific symbionts among the orchid fungi.

Lichens. — *Structural relations.* — A lichen is a plant complex made up of a fungus body in which algae are enclosed. Formerly lichens were supposed to be individual plants, and the green cells, now known to be algae, were called *gonidia* (figs. 417–419). The dual nature of lichens was discovered by making separate cultures of the constituent algae and fungi through entire developmental cycles. Also spores

from the fungus element of the lichen were sown among algae that had been growing separately in nature, and the developing fungus mycelium enclosed the latter, forming a lichen of the usual kind. Commonly the algal symbionts are well-known forms, such as *Pleurococcus* and *Nostoc*, but the fungi are most diverse and generally unlike other fungi, suggesting that considerable change may have been wrought in the latter through symbiosis. In fact, experiments have shown that lichen fungi when grown independently differ in form and in chemical composition from the same fungi when grown in symbiosis with algae. While the lichen body is that of the fungal symbiont, it is generally quite unlike ordinary fungus bodies, being flat, compact, and expanded like a liverwort. Since the algae make up what may be called the synthetic tissue, the advantage of the flat expanded surface is as evident as in liverworts.

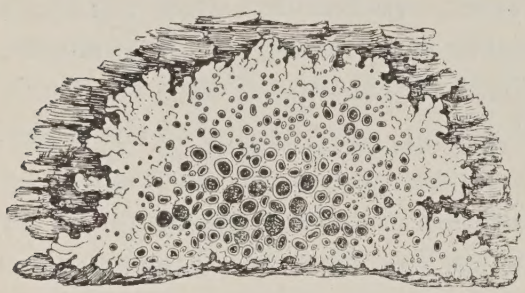


FIG. 417. — A foliose lichen (*Physcia*) on tree bark; note the marginal vegetative propagation characteristic of lichens, also the numerous fruiting structures, the apothecia. — From COULTER.

The autonomous features of lichens. — In spite of the proven duality of lichens, there are various things which suggest that they possess a high degree of autonomy or unity. It is quite conceivable that this autonomy might ultimately become so complete as to make impossible the separate cultivation of the two symbionts. Perhaps the most striking evidence of autonomy is afforded by the *soredia* (figs. 420–422), which are unique reproduc-

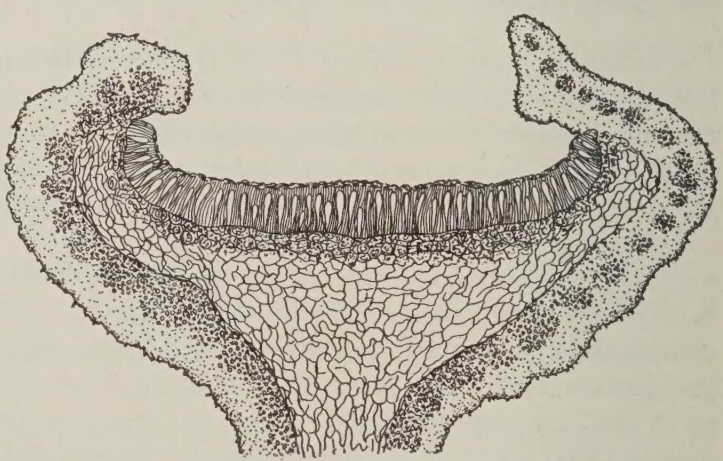


FIG. 418. — A section through an apothecium of a lichen (*Anaptychia*), showing the spore-bearing layer (hymenium), beneath which is the loose mycelium of the lichen body; these portions are in large part invested by the dense cortical mycelium with its numerous groups of algae; considerably magnified. — After SACHS.

tive organs consisting of a group of algal cells invested by fungal hyphae; at maturity the soredial structure buds off from the lichen thallus like a gemma (p. 323), forming, perhaps, the most efficient means of reproduction possessed by lichens, since the fungal spores are of value only when they happen to fall among appropriate algae. This is almost the only case where two symbionts have a common reproductive body. Another indication of autonomy is seen in the geographic distribution of lichens. As a class, they are among the most xerophytic and autophytic of plants, many species growing on the driest and barest of rocks, where few other plants can maintain themselves. Yet lichens are made up of algae, which as a group are characteristically hydrophytic, and of fungi, which as a group are characteristically mesophytic and dependent; the symbiotic union of two such diverse elements appears to result in a form widely different from either, and more resistant and independent than is to be found in almost any other group of plants.

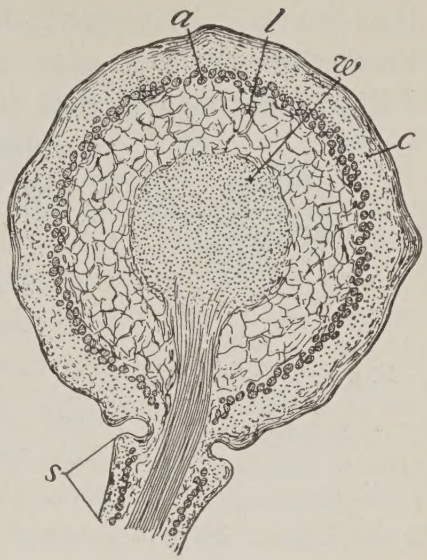
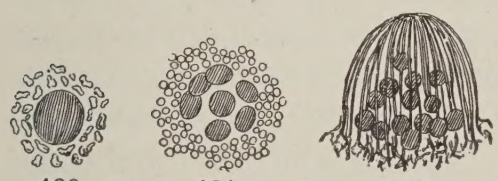


FIG. 419. — A cross section of a stem of the beard lichen (*Usnea barbata*) at the point of origin of a branch (*s*), the latter being shown in longitudinal section; *c*, cortical absorptive layer; *a*, algal layer; *l*, loose internal mycelium; *w*, an axial strand of densely placed hyphae, forming the highly elastic mechanical tissue of the lichen; highly magnified. — From SACHS.



FIGS. 420–422. — Soredia from the beard lichen (*Usnea barbata*): 420, a simple soredium, consisting of an algal cell, surrounded by a web of fungal hyphae; 421, a soredium in which the algal cell has reproduced by division; 422, a germinating soredium in which the algae are dividing, the hyphae forming an apex of growth; all figures highly magnified. — From SCHWENDENER.

The nature of lichen symbiosis. — The parasitism of the fungal symbiont upon the algal layer is undoubted, but there are various theories concerning the relation of the alga to the fungus. A common theory is that the relationship is one of *helotism* or slavery, the algal symbiont being represented as indifferent to the fungus. Another common theory is that of reciprocal parasitism, allied to which is the proposed theory of endosaprophytism, and also the older view

that the algae by living within the fungus body are better protected than when separate, and thus are enabled to live in drier habitats. Still another view is that the alga is merely the host of an ordinary parasite. The parasitism of the fungus is demonstrated clearly by a number of facts, such as the close embracement of algal cells by fungal hyphae (fig. 423), by the frequent entrance of hyphae into algal cells, by the occasional development of haustoria, by the disorganization and subsequent emptying of the contents of many algal cells, and, perhaps, by the apparent restriction upon algal activity, which is evidenced by increased vigor when released from symbiosis. As for the algal symbiont, the theory of endosaprophytism on fungal excreta seems most tenable in view of the fact that lichen algae are decided mixophytes which thrive particularly on peptones; water and salts must also be derived through the medium of the fungus.

FIG. 423. — An algal cell of a lichen (*Cladonia furcata*), which is closely embraced by hyphal filaments of the lichen fungus; highly magnified. — From BORNET.

The origin of lichens. — There is almost no experimental knowledge concerning the origin of lichens, and most of the common species appear to be well-defined lichens without obvious indications of their evolution. In some instances the fungal symbiont lives saprophytically on bark, or on humus or parasitically on the plant which gives it mechanical support, as well as on its algal layer; such species are most abundant in the tropics (p. 176), but some forms of temperate regions (*Usnea*, for example) may be partially parasitic on trees. A remarkable tropical lichen is *Cora pavonia*, in which the fungal symbiont, one of the Thelephoraceae, may live entirely apart from algae, or symbiotically either with the alga *Chroococcus*, or with the alga *Scytonema*, the body form differing in each case. The shape of this lichen varies also with the proportional development of the symbionts, the so-called genus *Dictyonema* representing a bracket-like form in which the fungal element dominates, while the so-called genus *Laudatea* represents a felt of filaments in which the alga (*i.e. Scytonema*) dominates. *Botrydina vulgaris*, which commonly is regarded as an alga, is invested by fungal hyphae, and is thought by some investigators to be a primitive lichen. A lichen such as *Cora* suggests that the fungal symbionts of other lichens may once have had facultative relations with algae, and also that the body form is very likely to have resulted from the symbiosis.

Green-celled animals. — Among the most remarkable of organisms are certain green-celled animals (such as *Spongilla*, *Hydra*, and *Convoluta*), which in some important respects resemble lichens. It has long been believed that the green cells represent enslaved algae, though, in contrast with the algal symbionts of lichens, separate cultivation generally is impossible. Indeed, the resemblance to algae is much less than in lichens, consisting of little more than the presence of chlorophyll; usually even the nuclei are absent from the cells, and the chlorophyll may be disseminated through the cell sap instead of being in plastids. Much light has been thrown on these strange organisms by a careful study of *Convoluta roscoffensis*, one of the flatworms. This animal is colorless when hatched, but in the first few days it becomes infected by motile algae (appearing to belong near *Carteria*), which seem to exhibit prochemotactic reactions to substances in the egg capsules. At first the animal has a mouth and feeds like other flatworms, but soon the opening becomes closed and the worm henceforth is completely dependent upon its symbiotic alga; even excretory organs are wanting in the adult, it being supposed that the algae utilize the excreta as a source of nitrogenous food. If the appropriate alga is absent in a culture of the worms, the animals soon die, even in the continued presence of such food as they previously have used. After imprisonment the algae lose their motility, though active cell division takes place for some time. The new cells have no cell walls, and eventually they become distorted; finally the nuclei disappear and all activity ceases. Such modified algae are unable to live apart from the worm, and the worm cannot live apart from the algae; indeed, the algae of adult worms cannot infect young worms, so that when they die, they leave no progeny. All doubt as to the reality of symbiosis has been removed by synthesizing the composite organism from pure cultures of the alga and the worm, precisely as lichens previously were synthesized from cultures of algae and fungi. While the exact nutritive interrelations are not certainly known, it has been shown that the mature animal with its green cells is prophototropic, and that starch is manufactured and oxygen given off in the sunlight. Since the animal has no other source of food, it clearly is parasitic on the alga. At first the animal uses the food (probably sugar) manufactured by the green cells, but ultimately it destroys the cells themselves and brings on thereby its own destruction. While it is possible that the alga utilizes substances in the animal (in which event the relation is one of reciprocal parasitism), it is quite as likely that the relation is to be regarded as a sort of destructive helotism, destructive because the enslaved organism is weakened and finally destroyed. In another flat worm, *Convoluta paradoxa*, the symbiotic alga is a unicellular brown species. Here the parasitism of the animal seems less obligate than in *C. roscoffensis*, since it continues to use its mouth in taking food, even after the symbiotic algae are well established in its body. However, the animal dies if it is kept in the dark until the algae are destroyed. While the origin of such symbiosis is unknown, it may be noted that in *Noctiluca*, one of the infusorians, symbiosis with green algae is facultative rather than obligate, thus suggesting a more primitive condition. Some of the sea anemones contain algae which are believed to be of nutritive importance to the animals, since the reactions of the latter to light resembles the reactions of algae rather than those of such sea anemones as are without chlorophyll. It is likely that the plants utilize the carbon dioxide given off by the animals, and that the animals in turn utilize the oxygen given off by the plants.

CHAPTER V — REPRODUCTION AND DISPERSAL

1. REPRODUCTIVE BEHAVIOR IN THE SEEDLESS PLANTS

General remarks. — The process by which organisms give rise to others of their kind is known as *reproduction*. The essential element in reproduction is the organization of a cell or a group of cells, which, if detached, possesses a capacity for independent development, and hence may be called *offspring*. Closely associated with reproduction is *dispersal*, which makes possible the development of organisms in new territory, and without which reproduction would be of small significance.[1] Detachable structures, however produced, if capable of dispersal, may be called *disseminules*, and it is obvious that upon such capacity for detachability and for subsequent mobility, the effectiveness of dispersal and therefore the success of a species must largely depend.

Most plants give rise to many new individuals within their lifetime, but only a few of these come to maturity and have progeny. The vast majority of plant disseminules fail to lodge in places suitable for development, while of those that make a start, but a very few ever reach maturity. The preëmption of space by other plants, the submergence of the weaker individuals, and untoward physical conditions cause the destruction of most plant offspring and prevent the otherwise rapid advance of any given species over the face of the earth. Three kinds of reproduction may be distinguished, each with its characteristic disseminules, namely, vegetative reproduction or propagation, reproduction by asexually formed spores, and sexual reproduction.

Vegetative reproduction. — *General characteristics.* — In *vegetative reproduction* or *propagation*, new plants are formed in connection with the vegetative organs, and the offshoots, sometimes known as *propagules*, more or less resemble the parts from which they issue. Vegeta-

[1] Dispersal without reproduction, though a conspicuous feature in animals, is relatively rare in plants; however, it is illustrated by certain motile algae (as *Chlamydomonas* and *Volvox*) and bacteria, and also by the amoeboid movements of myxomycete plasmodia.

tive reproduction is associated with periods of activity, while other forms of reproduction commonly terminate such periods. Vegetative disseminules differ from most other sorts in the relative absence of protective structures.

Vegetative reproduction in the algae. — The simplest form of reproduction is by *fission* or cell division, and is well illustrated by various unicellular algae, in which the mature cell divides, producing two or more new cells, which, whether cohering or becoming detached, represent new plant individuals (fig. 164). In most unicellular species the entire body takes part in propagation, so that the disappearance of the adult organism necessarily is coincident with the development of its progeny, though the original cell wall may remain for some time. Simple fission of this character is the only form of reproduction in unicellular blue-green algae and in some green algae (as *Pleurococcus*).

Many algae are filamentous, since division takes place only in parallel planes, and since the newly formed cells cohere (fig. 165). While such filaments have a certain individuality, the cells, at least in the lower algae, are essentially independent, and therefore to be regarded as potential individuals; hence as in unicellular forms, cell division may here be called vegetative reproduction, whether or not the new cells become detached from the old. True filamentous forms differ from unicellular species in that the adult does not necessarily disappear as its vegetative progeny develops. In the higher filamentous algae, cell coherence becomes a fixed feature, and the individuality of single cells is less marked, so that commonly a filament as a whole rather than one of its cells is regarded as a plant. Here the propagules rarely are single cells, but rather pieces of filaments that become detached. Even without such detachment, however, filamentous algae (such as *Spirogyra*) by continued elongation may spread so as to fill a pond in a relatively short time; branched forms like *Cladophora* would seem particularly suited for rapid propagation of this sort. In many blue-green algae the filaments break in rather definite places, the limits of the new filaments, the so-called *hormogonia*, being determined by cells differing from the rest, and known as *heterocysts*.

Vegetative reproduction in bacteria, fungi, and lichens. — Bacteria reproduce only by fission, yet they increase more rapidly than does any other group of plants. The possibility of rapid vegetative increase among the fungi is well illustrated by the growth of molds in moist chambers, where the hyphae spread quickly in all directions from the

original center (fig. 385). Often the fungus mycelium dies at its original growth center, perhaps because of the exhaustion of its food supply, but quite as likely because of the inhibitory effect of its own excretions. Subsequently the living mycelium forms an obvious ring of constantly increasing circumference, but whose thickness may not increase on account of the death of the inner hyphae *pari passu* with the advance of those outside. Such rings are common on pots in moist greenhouses. In some of the agarics, circles of toadstools, which are known as *fairy rings*, arise from subterranean mycelial rings, producing a striking effect. Sometimes fairy rings recur from a given mycelial center for many years; in a colony of *Hydnum suaveolens* that was observed for nine years, the diameter of the ring increased from seventeen to twenty-one meters, whence the age of the colony was estimated at about forty-five years. Sometimes similar circles of reproductive bodies, arising from rings of hidden mycelia, are associated with parasitic fungi (*e.g. Puccinia pyrolae*). Lichen thalli commonly spread radially from the original center of establishment, the advancing edge being lobate by reason of differential growth (fig. 417); frequently the older portions die as the newer parts spread out radially, producing living rings or bands, as in fungi.

Vegetative reproduction in the bryophytes. — Thallose liverworts, such as *Marchantia* and *Riccia*, spread radially from their original growth center (figs. 43, 44), after the manner of lichens. As the branches radiate outward and the posterior portions die, a number of individuals may arise from one by isolation; it has been shown that liverwort fragments which are only two millimeters in diameter can develop into a plant. Essentially similar is the propagation of foliose liverworts and of creeping mosses. Mosses increase vegetatively to a notable extent through the activity of their *protonema*, which is composed of branched alga-like filaments that creep along the soil surface much as do rhizomes. The protonemal filaments bear buds that grow into leafy plants, so that the area occupied by moss colonies is subject to constant radial extension. Mosses possess a wonderful capacity for propagation, almost any part of the leaves or stems (either gametophyte or sporophyte) being capable of giving rise to protonemal filaments under suitable conditions.

Vegetative reproduction in the vascular plants is of great significance, but has been considered in connection with roots and leaves, and particularly in connection with stems (p. 184).

Gemmation. — There is another kind of reproduction which generally is regarded as vegetative, although it grades insensibly into reproduction by asexual spores. *Gemmation* may be defined as the organization of vegetative buds that readily become detached from the parent plant; such disseminules are called *gemmae*. The simplest gemmae are unicellular, and they differ from asexual spores chiefly in the absence of a protective wall and of the resting period usually associated therewith, although there exist all intergradations between the two. Simple gemmae of this character are found in yeast, and also in *Mucor* and in *Vaucheria geminata*. Some species of liverworts also have unicellular gemmae on the leaf margins; in *Aneura* the gemmae are two-celled, and in *Marchantia* and *Lunularia* they are multicellular and are borne in clusters in special cupules (figs. 424, 425).

424 425

FIGS. 424, 425. — Liverwort gemmae: 424, a thallus lobe of *Lunularia vulgaris*, bearing a crescentic cupule in which are numerous gemmae; 425, a single gemma from a cupule of *Marchantia polymorpha*; considerably magnified.

Multicellular gemmae occur also on various mosses (as *Georgia pellucida*), on fern prothallia, and on some algae (as *Sphacelaria* and *Chara*). The soredia of lichens (figs. 420–422) also may be classed with gemmae. Certain structures in the vascular plants, such as the gemmae of *Lycopodium*, the leaf bulbils of ferns, the stem bulbils of lilies, and the inflorescence bulbils of the onion (p. 418) are comparable to the gemmae of the lower plants.

FIG. 426. — A sclerotium (*s*) of the ergot fungus (*Claviceps purpurea*), growing from a spikelet of the sand-reed (*Ammophila arenaria*).

Sclerotia. — In autumn the mycelium of the ergot fungus (*Claviceps*) becomes enveloped in a dense and relatively impermeable protective layer of dark, thick-walled cells, within which the vegetative hyphae remain dormant over winter; the entire structure, which is richly packed with food, is called a *sclerotium* (fig. 426). In spring the sclerotium germinates, and ordinary vegetative activity is resumed. Somewhat similar to the sclerotia of ergot are those of *Peziza sclerotiorum* and of various other fungi. Many fungi (*e.g. Sclerotinia*) have subterranean tuber-like sclerotia richly packed with food, which endure through unfavorable periods, and other forms have tough sclerotial strands resembling shoestrings. In the myxomycetes the plasmodium or a part of it may become encysted into a sclerotial mass and remain dormant even for years. While strictly vegetative tissue is involved in the formation of sclerotia, they agree with spores and seeds in being formed at the close of vegetative periods and in being fitted for existence in a dormant state during severe periods. Comparable to sclerotia are

the resting cells of bacteria, the thick-walled resting cells of *Nostoc* which are closely packed with food, the starchy tubers of *Chara*, and the subterranean resting buds of liverworts and mosses.

Auxospores. — In the diatoms vegetative reproduction takes place by longitudinal splitting, but each new individual often is shorter than the last, because it is formed within the old and rigid siliceous wall. In time progressive diminution ceases, and the protoplast escapes, whereupon it enlarges to the original size and again becomes incased by rigid siliceous walls. The enlarging protoplast is called an *auxospore*.

The significance of vegetative reproduction. — Vegetative propagation is the most universal kind of reproduction. Some plants (as the bacteria and lower algae) have no other kind, while very few plants (*e.g.* some annuals, biennials, and trees) are altogether without it. Many plants that are capable of producing spores or sex organs nevertheless spread almost wholly by vegetative means; among such plants are many mosses, some liverworts (as *Lunularia*), and even some of the higher plants (as the duckweeds). In far northern regions many plants are said to reproduce as a rule only vegetatively, the summer being too short for seed production. Even those plants that fruit regularly usually spread much more by vegetative propagation than by spores or seeds. Thus there can be no doubt that vegetative reproduction is the chief factor in the maintenance of species and in the enlargement of their areas.

The chief disadvantage associated with vegetative reproduction is that propagules rarely are fitted for distant dispersal. Hence the invasion of new areas by this means alone is slow; the ultimate establishment of a species by vegetative reproduction in a distant region is even impossible unless favorable habitats are continuous, since propagules rarely are able to cross barriers. For example, the rhizomes of mesophytes (such as the Solomon's seal and various ferns) are unable to migrate over bodies of water or dry ridges, although such migration may be accomplished quickly by most spores and by many seeds. Sometimes, however, propagules are true disseminules, notably among the water plants, where portions of plants may become detached and float for great distances, thus equaling seeds in mobility and in the widespread invasion of new regions. Among land plants the distant dispersal of vegetative disseminules is confined chiefly to gemmae; the minute gemmae of various liverworts may be scattered for some distance by wind, and lichen soredia are scattered almost as effectively as are spores.

Reproduction by asexually formed spores. — *General characteristics.* — *Asexually formed spores* [1] commonly are unicellular structures (multinucleate in *Vaucheria*), produced, as a rule, by specialized spore-bearing organs (*sporangia*, etc.; see Volume One). Generally they differ from gemmae in their unicellular nature, in their production by specialized organs, and in their capacity for endurance, which often is increased by the presence of thick protective walls; however, hard and fast lines are not to be drawn, since some spores are incapable of enduring severe periods, while gemmae may be unicellular or borne by special organs.

Reproductive structures generally have one or more of three characteristics: capacity for increasing the number of individuals in a species (which is, of course, the primary feature of reproduction); capacity for endurance through severe periods; and capacity for dispersal. Asexual spores are efficient in all three respects, thus contrasting with propagules, which have been seen to be relatively ineffective as disseminules and often unfitted for endurance, though they are the most efficient of all means of multiplying individuals. Asexual spores occur in nearly all plant groups, though they are unknown in various algae (as in the Conjugales, Fucales, and Charales), and are practically absent in some higher plants (as in various mosses and in the duck-weeds).

FIG. 427. — A zoospore or swarm spore of the water-net (*Hydrodictyon*); note the two cilia which effect locomotion; highly magnified. — After TIMBERLAKE.

Asexual spores in the algae. — The most representative asexual spores among the algae are the *zoospores* or swarm-spores, which differ from most spores in being without protective walls, and whose chief distinguishing character is the power of locomotion in water; usually they move by means of variously arranged cilia, which may be single (as in *Botrydium*), two (as in *Hydrodictyon*, fig. 427), four (as in *Ulothrix*, fig. 439), or many (as in *Oedogonium* and *Vaucheria*). While most characteristic of green algae, swarm-spores occur in some of the brown algae (as in *Ectocarpus*). Zoospores are among the most efficient of reproductive structures, partly because commonly they are produced in large numbers, but particularly because they differ from almost all other disseminules in exhibiting directive dispersal. For example, they are prophototactic, hence they usually move to a well-

[1] Often these are called for convenience *asexual spores* or simply *spores*.

lighted situation where they may germinate into new plants under favorable conditions. The lack of protective walls is hardly a disadvantage, since zoospores are not exposed to transpiration, nor are they obliged to live over unfavorable seasons. In the red algae true zoospores are wanting, though a few species have spores that exhibit amoeboid movements; much more characteristic are non-motile *carpospores* and *tetraspores*, which, like zoospores, are devoid of protective walls. Non-motile spores may occur also in the green algae (as in the aplanospores of *Botrydium*).

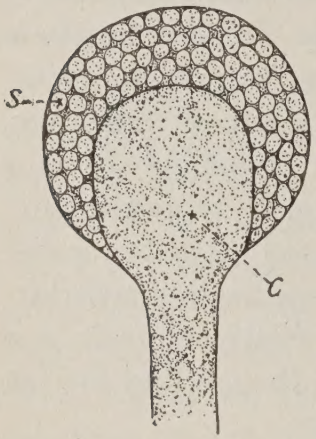


FIG. 428. — The sporangium of a mold (*Mucor*), showing the columella (*c*) and numerous spores (*s*); highly magnified. — From COULTER.

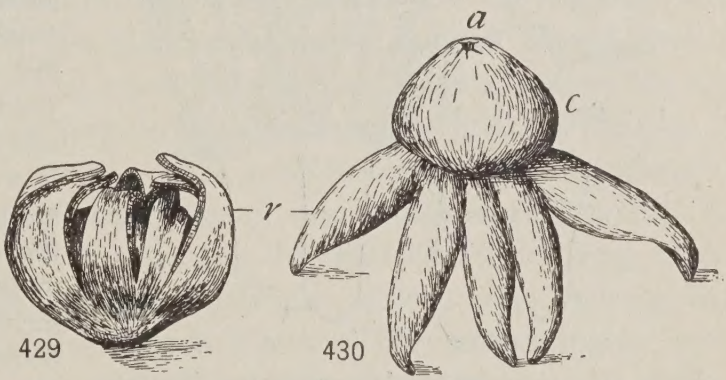
Asexual spores in the fungi. — Perhaps the culmination of asexual spore development occurs in the fungi. A few forms that grow in water or in wet places have ciliated zoospores (as in *Saprolegnia*); in certain myxomycetes there are zoospores which swim for a time, and then lose their cilia and creep with an amoeboid movement. In general, however, fungus spores are not self-motile, and are invested with conspicuous walls. They may be borne within a special spore-bearing organ, for example, a *sporangium* (as in *Mucor*, fig. 428), or an *ascocarp* (as in *Peziza*), or they may be developed externally, as in the *conidia* of *Penicillium* and in *basidiospores*.[1]

Fungus spores commonly are dispersed by wind, and their minute size and their resistance to wetting make possible the remarkable efficiency of this agent; even the very slightest movements of the air are sufficient to initiate dispersal. Many species of fungi are common to widely separated regions, and it is thought that this cosmopolitanism is due in large part to the effectiveness with which their spores are dispersed by wind. The abundance of spores and the ease with which they are carried is shown by the readiness with which cultures of various fungi may be made anywhere by exposing to the air, bread or cheese, properly moistened, so as to insure good conditions for germination. Fungi surpass all other plants in the number of new individuals that may be produced from a single plant by asexual spores. A single large puffball (as *Lycoperdon giganteum*) may produce several trillion spores,

[1] Basidiospores, however, though actually external, in the mushrooms are considerably protected by the fruit body on which they develop.

and in other large fungi their number may run well into the billions. The production of spores in such great numbers is advantageous, since generally only a single spore in many millions falls in a place where it can develop into a plant.

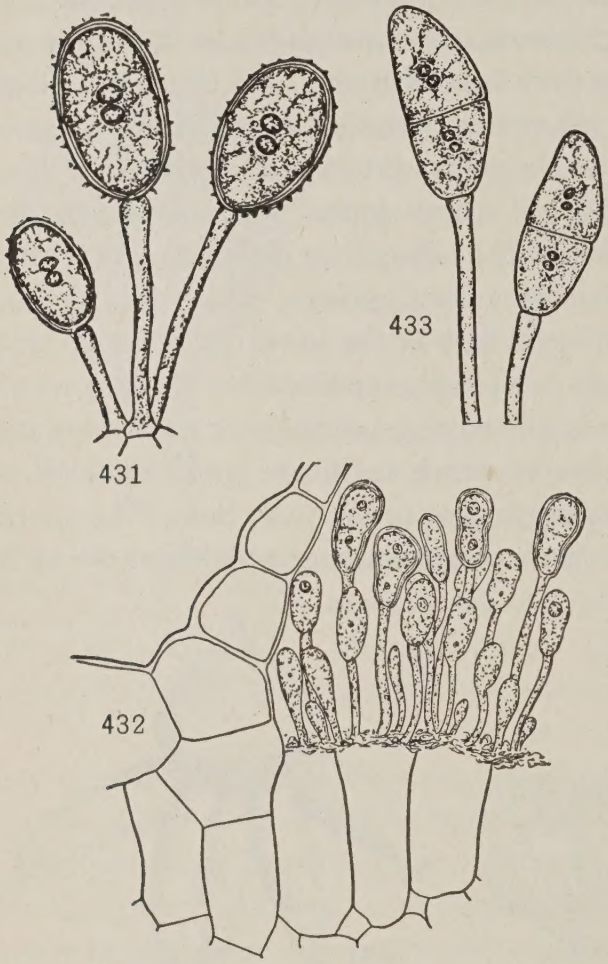
Various features of structure or habit facilitate spore dispersal. As previously noted, many fungi bear spores externally, so that they are readily blown away as soon as they are abstricted. In the fleshy fungi, the spore-containing organs often are borne on conspicuous apogeotropic *stipes*, which thus elevate the spores into a good position for wind dispersal (fig. 385). In many of these forms the spores are discharged from the gills, after which they drop into positions where they may be wafted off by air currents. In *Coprinus*, which has a cylindrical fruit body, the spores mature first in the lower part, which then curves outward, and hence does not hinder the dispersal of those which ripen later. Where spores are borne within sporangia or similar organs, there often are no special features which facilitate spore removal, it being necessary for the enveloping organs to rot away before the spores can be dispersed. In some cases there is definite dehiscence, as in *Geaster*, where the sporangial wall (*peridium*) has two layers, of which the outer splits into star-shaped segments (whence the common name, earth star), while the inner has an apical opening (fig. 430); in the related puffballs the outer layer breaks irregularly. In *Geaster* the hyphae are arranged at right angles to the surface in the inner (*i.e.* upper when open) part of the ray and parallel to the surface in the outer part. Hence in moist weather the inner part absorbs the more water and the rays open (fig. 430), while they close in dry weather (fig. 429), since the inner part loses the more water. This hygroscopic mechanism has been thought to facilitate spore dispersal; the dry



FIGS. 429, 430. — An earth star (*Geaster hygrometricus*); 429, a fructification, as seen in dry weather, the peridium rays (*r*) being incurved about the spore-bearing portion; 430, a fructification, as seen in moist weather, the peridium rays being expanded; note the aperture (*a*) through which the spores escape.

closed structure is bowled along by the wind like a tumbleweed, and the rain washes out spores from the opened structure.

In a few fungi, spores are scattered by agents other than wind. In *Pilobolus* the columella of the sporangium ultimately bursts by reason of increasing turgor, whereupon the escaping water tears loose the sporangium and expels it with the enclosed spores for some distance. In a somewhat similar fashion are expelled the conidia of *Entomophthora* and the ascospores of *Ascobolus* and of *Peziza repanda*. In the ergot fungus (*Claviceps*) a sweetish substance, known as *honey dew*, is secreted as the conidia ripen, and insects visiting the fungus for the honey dew scatter the spores. In the stinkhorn fungus (*Phallus impudicus*) the spore-bearing portion deliquesces into a vile-smelling mass that attracts flies, which scatter the spores. Doubtless many fungus spores also adhere to the slimy surface of slugs and thereby are scattered. Flies are among the most efficient scatterers of spores, which become attached to various parts of the body, and occur abundantly in the excreta; the spores or propagules of more than fifty species of fungi and bacteria have been found in a single fly speck.



FIGS. 431–433. — Spores of the wheat rust (*Puccinia graminis*): 431, uredospores; 432, young teleutospores; 433, mature teleutospores; note that the uredospores are one-celled, and the teleutospores two-celled; highly magnified; 431, 433 from COULTER; 432 from CHAMBERLAIN (Vol. One).

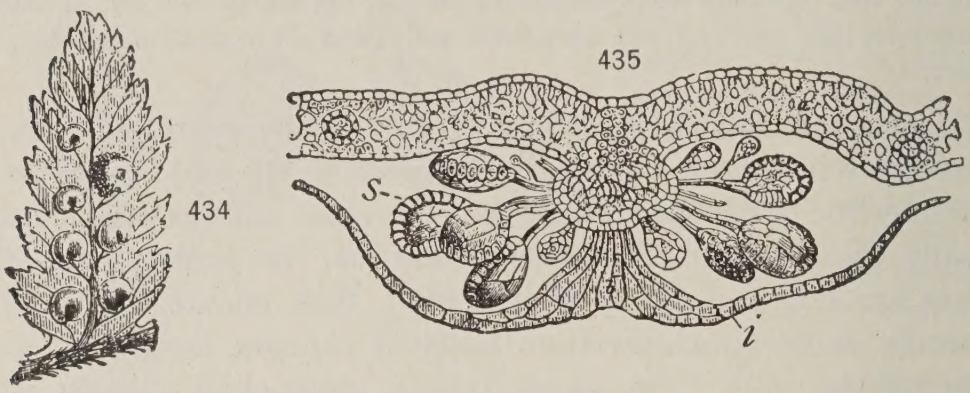
Many fungus spores are able to endure severe conditions. For example, the spores of *Mucor* and of *Aspergillus* have been dried for two years, after which they were exposed for three weeks to a temperature of − 180° C., and for three days to − 253° C., without impairing their capacity for germination. Desiccated bacteria have been known to retain their vitality for nearly a hundred years. It is concluded from such experiments that all vital activity may be suspended for long periods of time (p. 424). In part this endurance is due to unexplained features in the resting protoplasm, but there are also many instances of protective structures or habits. In most ascomy-

cetes the spores, though thin-walled, are protected within the ascocarps (as in lichens and mildews), while in many hymenomycetes the thin-walled basidiospores are protected by the pileus; some of the so-called bracket fungi are hard and woody and capable of enduring the winter. In the heteroecious rusts there are borne in spring and summer basidiospores, *aecidiospores*, and *uredospores* (fig. 431), all with relatively thin cell walls, while toward the close of the season there are developed *teleutospores* (figs. 432, 433), which are thick-walled and are capable of enduring the winter.

Asexual spores in the bryophytes. — In most liverworts and mosses there is a well-defined *alternation of generations* (p. 337), spores being characteristic of one generation, the *sporophyte*, and sex organs being equally characteristic of another generation, the *gametophyte*. The spores are scattered chiefly by the wind, their minute size and the generally stalked and therefore elevated *capsules* facilitating such dispersal (fig. 285). The spores contain chlorophyll, so that independence is possible from the outset, if the *sporelings* (*i.e.* the germinating spores) are exposed to light. Sometimes (as in *Riccia* and *Phascum*) the spores are exposed to dispersing agents only upon the decay of the capsule wall, but more commonly there is definite dehiscence. In the Jungermanniales and in *Anthoceros* the capsule wall splits into *valves*, and in the Marchantiales and in most mosses there is a *lid* or *operculum*. Most moss capsules are fringed toward the tip with a *peristome*, whose hygroscopic teeth open when the weather is dry and close when it is moist; these movements effect the detachment of the operculum, and probably are of some value in facilitating the removal of spores from the capsule. In most liverworts long, fiber-like, spirally thickened bodies, known as *elaters*, occur among the spores, and, like the peristome teeth of mosses, they exhibit hygroscopic movements which are thought to facilitate spore removal. As a rule, the spores of liverworts soon lose their capacity for germination, but the spores of mosses may retain their vitality for a long time; cases are on record where moss spores have germinated, after having lain dry in a herbarium for fifty years.

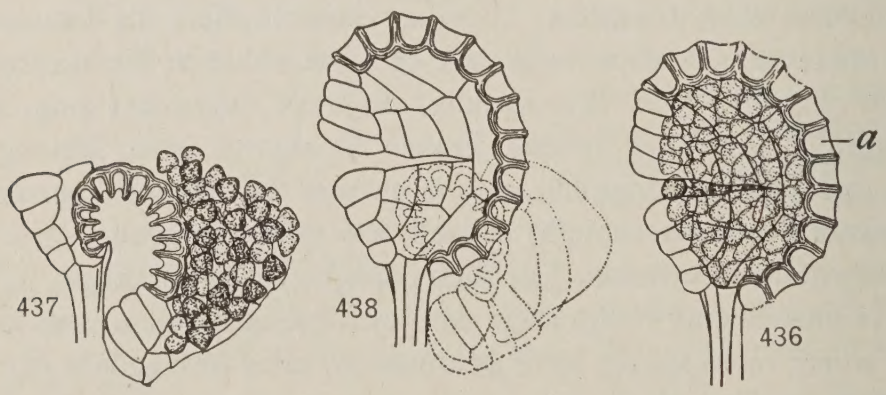
Asexual spores in the pteridophytes. — In the Filicales the spores commonly are borne in sporangia on the backs of ordinary foliage leaves (figs. 434, 435), but in some cases (as in *Onoclea* and *Osmunda*) special leaf regions or entire leaves are spore-bearing, while other leaf regions or entire leaves are foliage organs; comparable to the latter are the Ophioglossales. In *Equisetum* the sporangia are borne on a special structure, the *strobilus*, and, as in liverworts, there are elaters which

assist to some extent in dispersal. In *Lycopodium* the sporangia may be arranged in the axils of foliage leaves or in a strobilus. In the above pteridophytes all the spores are alike, that is, *homosporous*, but in the water ferns (*i.e. Marsilea*, *Salvinia*, and *Azolla*) and in *Selaginella* and



FIGS. 434, 435. — Reproduction by asexual spores in a fern (*Aspidium*): 434, a leaf segment (pinnule) with fruit dots (sori), each with a shield-shaped cover (indusium); 435, a cross section through a sorus, showing the indusium (*i*) and long-stalked sporangia (*s*); 435 considerably magnified. — After WOSSIDLO.

Isoetes there are two kinds of spores, namely, small spores or *microspores*, and large spores or *megaspores;* such a condition is known as *heterospory*. Upon germination the microspores give rise to male plants and the megaspores to female plants, whereas the spores of



FIGS. 436–438. — Dehiscence of a sporangium in a fern (*Polystichum acrostichoides*): 436, the sporangium cracked; *a*, the annulus; 437, position of reversal, exposing the spores; 438, position after recoil, the sporangium having been emptied; highly magnified. — After ATKINSON.

most homosporous ferns give rise to plants that bear both male and female organs.

The spores of most pteridophytes are scattered by the wind, and they are well fitted for such dispersal by their small size, by their resistance

to wetting (particularly in *Lycopodium*), and by their elevation upon foliage leaves or special stalks. Fern sporangia dehisce in a somewhat complicated manner, a ring of dead tissue, the *annulus*, springing back and releasing the spores when a certain stage of desiccation is reached (figs. 436–438). Probably no other vascular plants equal homosporous pteridophytes in their capacity for dispersal; the great wealth of ferns on oceanic islands commonly is explained by the easy dissemination of their spores by wind.

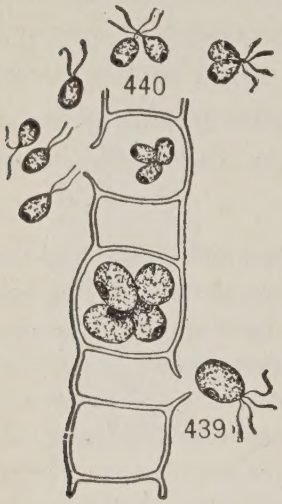
In *Salvinia* there is no true dehiscence, the whole sporangium being shed and the spores germinating within. In *Azolla* the sporangial wall slowly decays, setting free the spores. In *Marsilea* the spores are contained within a hard-walled structure, the *sporocarp;* when moistened the internal mucilaginous tissue absorbs water and it swells to such an extent as to burst the sporocarp wall and protrude into the water, carrying with it the attached sporangial masses. In heterosporous pteridophytes the microspores have the mobility characteristic of the spores of homosporous forms, but the megaspores are much less mobile; indeed, in some species of *Selaginella* mobility is entirely absent, and the megaspore no longer is a disseminule. With regard to protection and endurance, spores may vary from the relatively delicate chlorophyll-containing spores of *Equisetum*, which die unless germination occurs at once, to the remarkably protected spores of *Selaginella*, which commonly germinate only after a long resting period. Remarkable resistance to severe conditions is shown by the spores of *Marsilea*, which have been known to germinate when sporocarps that had been kept dry for eighteen years were placed in water; much of this capacity for endurance is due to the impermeability of the sporocarp wall, as is shown by the fact that the spores in sporocarps that have been kept in alcohol for three years may still remain capable of germination.

In the seed plants there is an extremely complicated situation. Heterospory is there universal, and the microspores (better known as pollen grains) are scattered by various agents. The megaspores, however, always are retained, having no longer the character of disseminules. The ecological features of these organs will be considered in connection with flowers (p. 340).

Sexual reproduction. — *Significant features.* — The chief feature of sexual reproduction is the union or fusion of two cells, known as *gametes*, resulting in the production of a sexually formed spore. Usually the two gametes may be distinguished as male cells or *sperms*, and female cells or *eggs*. The spore resulting from fusion, upon germination, develops into a structure called the *embryo*.

Isogamy. — In those thallophytes in which sexuality seems to be just beginning (*e.g. Ulothrix*, figs. 439, 440), the two gametes are similar in size and in structure and usually in activity; such a condition is called *isogamy;* the spore resulting from the fusion of equal gametes is called a *zygospore*. Isogamous gametes may be ciliated and

actively motile (as in *Ulothrix*), non-ciliated but somewhat motile (as in the diatoms), or almost immotile, that is, not leaving the plant body. Although isogamous gametes exhibit no structural differences, there is some evidence of unlikeness; for example, in *Ulothrix* and in *Acetabularia*, fusion takes place only between gametes from different gamete-producing organs (*gametangia*), and in *Dasycladus*, only between gametes from different plants, though it is impossible in any of these to distinguish male and female characters. However, in the Conjugales, one of the gametes often is immotile, while the other migrates from a neighboring filament through a passageway made by the fusion (or conjugation) of two lateral outgrowths. From analogy with the higher plants, the immotile gamete may be called female and the motile gamete, male. In some conjugating forms, as *Mucor*, there is no such distinction, the two gametes moving equally and meeting in the passageway between the filaments. Usually zygospores are thick-walled resting cells closely packed with food and well able to exist over severe periods.



FIGS. 439, 440. — Zoospores and isogamous gametes in *Ulothrix:* 439, a part of a filament from which a 4-ciliate zoospore and several smaller biciliate gametes are escaping; 440, gametes pairing and fusing; highly magnified. — From COULTER.

Heterogamy. — In the great majority of plants, including many thallophytes and all the higher plants, the two gametes are unequal; this condition is known as *heterogamy*, and the spore resulting from the fusion of unequal gametes is called an *oospore*. It is in the heterogamous plants that one may speak of true sex differentiation and of the development of male gametes or *sperms* and of female gametes or *eggs* (fig. 441). In nearly all bryophytes, pteridophytes, and heterogamous algae the sperms are relatively small, ciliated, actively motile bodies, whereas in the seed plants (except in *Ginkgo* and in the cycads), they are non-ciliated, and exhibit but little true locomotion. Eggs commonly are much larger than sperms, and, except in the case of a few algae where they float freely in the water, they are essentially immotile.

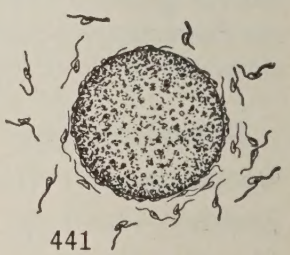


FIG. 441. — Heterogamy; an egg of *Fucus*, surrounded by a swarm of biciliate sperms; highly magnified. — After THURET.

Often the male and female gametes are borne in special organs, the *antheridia* and the *oogonia* (or *archegonia*), respectively. In many thallophytes the oospore is a thick-walled resting cell.

Of chief ecological interest in connection with heterogamy are the factors concerned in facilitating the fusion of gametes and particularly the fusion of gametes of different immediate ancestry. In the algae as a group, fusion is comparatively easy, since the eggs are immersed and the sperms capable of locomotion. In the bryophytes and pteridophytes the difficulty is greater, because usually they are land plants. In the liverworts and ferns the gametophytic generation commonly grows close to the moist soil, where there often is sufficient moisture for the swimming of such minute bodies as sperms. In many cases the female organs contain substances which occasion prochemotactic reactions in sperms, thus greatly facilitating the fusion of gametes; among such substances are cane sugar (as in mosses) and malic acid (as in ferns).

Monoecism and dioecism. — When the same individual bears correlative kinds of reproductive organs (*e.g.* antheridia and archegonia, or stamens and pistils), the species is called *monoecious* if the organs are borne on separate branches, and *hermaphroditic* if the organs are borne together on a common branch; if the two kinds of organs are borne on separate individuals, the species is called *dioecious*. In the heterosporous pteridophytes dioecism occurs regularly, male gametophytes developing from microspores and female gametophytes from megaspores. In most homosporous pteridophytes the gametophytes are monoecious, but they are chiefly dioecious in *Equisetum*, and there are many dioecious species among the algae and bryophytes. Obviously the movement of sperms to the female organs is easier in monoecious than in dioecious species. It has been supposed that the chief advantage of dioecism is that it prevents close inbreeding (*i.e.* fusion between closely related sex cells), it being believed oftentimes that certain advantages are associated with the fusion of gametes of different immediate ancestry (see p. 335). In the homosporous pteridophytes the fusion of related gametes often is impossible, since many species are *dichogamous*, that is, with the correlative organs on the same individual maturing consecutively; commonly the male organs develop first.

In some dioecious species there are features that facilitate the germination of male and female plants in close proximity; for example, the elaters of *Equisetum*

often cause a group of spores to become intertangled and thus to fall and germinate together, and in *Azolla* the microspores cohere in masses and often have hooks, the so-called *glochidia*, which become caught in the projecting filaments of the megaspores. However, in many cases dioecism doubtless is disadvantageous because of the difficulties in the way of fusion between male and female gametes. In many mosses sporophytic generations rarely are seen, partly, perhaps, because of dioecism, and partly, it may be supposed, because the elevated female organs make more uncertain the presence of sufficient water for sperm motility. In hermaphroditic mosses dichogamy is rare, hence close inbreeding is the rule rather than the exception.

The advantages and disadvantages of heterospory. — In heterosporous pteridophytes the proximity of male and female gametes is a matter of uncertainty, since it depends upon the chance of microspores and megaspores lodging near one another. In most living species the difficulty, perhaps, is slight, since the plants are so small that often the spores must fall near the parent plant and hence near each other; furthermore a number of the species are hydrophytes, and hence the motile sperms have a favorable medium. In past ages, however, there have been many heterosporous trees among the pteridophytes, and the waste of both microspores and megaspores must have been enormous. This is the only known ecological group of past ages that is unrepresented among living forms, and it well may be that its disappearance was due in part, at least, to its disadvantageous heterospory, coupled, perhaps, with extensive land emergence and with the consequent lessening of habitats favorable for the fusion of gametes. In contrast with this extinct group are the seed plants, whose greater success probably is due in part to the retention of the megaspores instead of their dispersal, with the enormous consequent waste; the waste even of microspores is reduced largely in the great group of insect-pollinated plants. However, the seed plants do not equal the homosporous ferns and the lower plants in ease of dispersal, as appears from the fact that the homosporous constituents of any two widely separated floras are much more alike than are their heterosporous constituents. Obviously the great advantage of heterospory, if such there be, must be sought along other lines, even in the seed plants.

The significance of sexual reproduction. — In the simplest cases (as in *Ulothrix*) the result of the fusion of gametes is a decrease of potential individuals, since two cells resembling zoospores and having, perhaps, the possibility of growing into two plants unite and form a spore that can grow into but one plant. However, since a single algal filament may produce a number of gametes, considerable multiplication is

possible through sexuality; this is conspicuous especially in those groups which are without asexual spores (*viz.* the Conjugales, Charales, and Fucales). But in plants with a well-defined alternation of generations (*viz.* in bryophytes, ferns, and seed plants) sexual reproduction rarely results in a significant increase of individuals, asexual spores or propagules chiefly being responsible for such increase.[1] Thus multiplication, which is the feature of chief significance in other forms of reproduction, usually is not conspicuous in sexual reproduction. Gametes and the spores resulting from their fusion (except in the thallophytes) are among the most delicate of plant structures, so that fitness for endurance through severe periods is not one of their characteristics, as it is of many asexual spores. Furthermore, neither the gametes nor the resulting spores are particularly efficient disseminules; the female gamete, in particular, whose position determines the place of the next generation, is for the most part immotile. Hence none of the three features commonly associated with reproduction, namely, multiplication, endurance, and dispersal, are of especial significance in sexual reproduction.

It is believed commonly that sexual reproduction makes possible the advantageous merging in one individual of the qualities of two races, hence sometimes the phenomenon is known as *amphimixis*. In *Ulothrix* the advantage gained has been thought to be one of size, since plants developing from zygospores are larger than those which develop from gametes that fail to fuse. In other cases (apart, perhaps, from seed plants, p. 382) the advantages of sexuality appear more hypothetical than real, but even hypothetically the crossing of two races might fairly be expected to introduce into a given strain disadvantages as well as advantages. The chief reason for believing that sexuality is of no particular advantage (at least in the lower plants) is that its absence seems to bring no disadvantage. In the bacteria and blue-green algae, in some green algae, and in many fungi, true sexuality is absent, but no plants are more successful than these; in many fungi (as in *Saprolegnia* and in the Ascomycetes), and in some liverworts and mosses there is excellent evidence of diminishing sexuality (see p. 400), but none of

[1] Such increase as there is among these plants is most conspicuous among the bryophytes, where single gametophytes may bear several (rarely many) sporophytes. Sometimes (especially in gymnosperms) two or more embryos develop from one sexual spore or from one sporiferous center of a gametophyte, a phenomenon known as *polyembryony;* this is of little significance, however, inasmuch as but one embryo, as a rule, is able to mature.

diminishing success.[1] Even in the higher plants, where sexuality is much more general, no demonstrable loss comes from its elimination in those cases where vegetative reproduction is well-developed, and such cases constitute the vast majority. In various seed plants (as the duckweeds) sexual reproduction rarely occurs, and many economic plants (such as the banana, the fig, and the sweet potato) have been propagated almost from time immemorial solely by vegetative means and yet without obvious deterioration. A second theory claims that sexuality insures rejuvenescence. However, this is insured much more generally and economically through propagation and asexual reproduction. A third theory is that sexuality favors variation and therefore evolution through the repeated mingling of new elements, thus giving rise to new combinations of characters and hence to new species. This view seems reasonable, but there is little positive evidence in its favor. Furthermore, variation is known to be of frequent occurrence in the bacteria and blue-green algae and in other sexless groups; indeed many investigators hold that crossing promotes fixity rather than variation, and it has been shown that in inbred races of *Spirogyra* and *Phaseolus* the amount of variation is as great as or greater than in cross-bred races. Sometimes the theory is advanced that the significance of sexuality lies in the fusion of kinetic and trophic (*i.e.* nutritive) elements; the egg is regarded as having the food necessary for development, while the sperm adds the requisite developmental stimulus. These kinetic and trophic rôles are not to be doubted, but they furnish no clew to the significance of sexuality, giving rather an explanation of embryo development. In propagules and in asexual spores both kinetic and trophic elements are present in sufficient degree to insure development, so that in these respects sexuality adds nothing new. At present no theory as to the rôle of sexuality has much support. It is not impossible that it is a necessary accompaniment of evolution but without particular significance, although in the entire plant kingdom there probably is no other equally widespread phenomenon which is

[1] There have been discovered modified forms of sexuality in the rusts and smuts and in various other fungi, but in these cases there is no crossing, so that true amphimixis with its supposed advantages necessarily is excluded. In many algae, there occurs inbreeding or *automixis*, which is well illustrated in *Spirogyra*, where fusion may take place between gametes of adjoining cells in the same filament, and in *Ulva*, where fusion may take place between sister gametes arising from a common cell. In some ferns (as *Lastrea*) and in various fungi, the fusing structures are thought to be vegetative rather than sexual; in contrast to amphimixis and automixis such fusion has been termed *pseudomixis*.

without conspicuous advantage. The most that can be said with certainty concerning the advantage of sexual reproduction among the lower plants is that it supplements the other and more successful kinds.[1] As to the plants above the thallophytes, there remains to be considered the alternation of generations.

The significance of alternating generations. — The chief advantage in the alternation of generations has been supposed to be that one generation, the sporophyte, produces asexual spores in great abundance, thus facilitating multiplication and dispersal, while the other generation the gametophyte, produces gametes, thus facilitating the merging of characters of different individuals. The advantages of the sporophytic generation are obvious enough, but those of the gametophytic generation are less apparent, depending solely upon such advantages as may inhere in sexuality. There are some obvious disadvantages in alternation; for example, in certain mosses, as previously noted, the conditions for the fusion of gametes often are lacking, hence development is impossible for the sporophyte with its numerous asexual spores, however well-fitted they may be for multiplication and dispersal. In the ferns, where considerable moisture is required by the gametophytic generation and particularly for the fusion of gametes, the sporophytic generation, which often is well-suited for xerophytic situations, can grow only where a gametophytic generation has preceded it.[2] In the seed plants, the alternation of generations means that seed formation, in addition to favorable conditions in the soil and the climate, depends upon pollination, and therefore upon various pollinating agents, such as wind and insects.

[1] In *Paramecium*, one of the infusorians, individual animals reproduce ordinarily by simple fission. After a time, individuals of one line of ancestry conjugate with those of another, and there appears to be an exchange of substance between the individuals, which later separate and again reproduce by fission. Since cultures of *Paramecium* in which conjugation does not take place show a gradual decrease in size and activity after many generations, it has been urged that sexuality thus is shown to be advantageous, at least in animals. Indeed, in the older experiments, cultures in which conjugation was prevented could not be maintained for more than 140 generations (*i.e.* about three months), although parallel cultures with conjugation remained vigorous indefinitely. More recently it has been shown that it is not lack of conjugation which causes death, but probably some deterioration in the culture media, since by varying the media from time to time, 1500 generations have been secured without conjugation and with no loss of vigor. It is now believed that cultures of *Paramecium* thus can be kept indefinitely without conjugation, and it is to be noted that the changes introduced in the culture media probably are much less than are those which occur in natural habitats.

[2] Of course such a plant as *Pteris* may migrate from its place of origin by rhizome propagation.

Apogamy and apospory. — In some cases one of the alternating generations is eliminated in whole or in part; if the eliminated structure or process is gametophytic, the phenomenon is called *apogamy;* if sporophytic, it is called *apospory.* In *Pteris cretica*, *Nephrodium molle*, and in many other ferns the sporophyte may develop from a bud on the gametophyte; here gametophytes but not gametes appear to be necessary for sporophyte development. In *Coelebogyne* (one of the seed plants) certain cells of the sporophyte nucellus are able to develop into embryos, the entire gametophytic generation thus being unnecessary for seed production. Apogamy is now recognized in a number of seed plants, as in *Euphorbia*, *Allium*, *Elatostema*, and *Balanophora;* in *Coelebogyne*, in *Balanophora*, and in *Euphorbia dulcis* there is no necessity for sexual fusion; in *Elatostema* there is no egg, and in *Balanophora globosa* even the staminate flowers are wanting. Apospory is illustrated in certain ferns, in which the gametophytic generation may develop from sporangia (as in *Asplenium*) or even from vegetative parts of the leaf (as in *Polystichum*). There are some varieties of ferns and of seed plants which exhibit both apogamy and apospory, their reproduction being wholly vegetative. The chief advantages of apogamy and of apospory would appear to be that they eliminate the disadvantages of alternating generations.

Parthenogenesis. — The development of a gamete into a plant without fusing with another gamete is known as *parthenogenesis.* The egg is much more likely to develop parthenogenetically than is the sperm, probably because of its greater size and more abundant food supply.[1] In such forms as *Ulothrix*, where a gamete almost indifferently either may fuse with another gamete or develop independently, or in *Ulva*, where small gametes commonly fuse and certain of the larger gametes usually develop without fusion, parthenogenesis probably represents the retention of a primitive character; perhaps the same is true in *Zygnema.* The significance is quite otherwise in *Saprolegnia*, where parthenogenesis is accompanied by all stages in the abortion of the male organs, from almost complete development to the entire absence of the antheridium. Other plants in which parthenogenesis has been reported are *Chara crinita*, *Marsilea*, *Thalictrum*, *Alchemilla*, *Wikstroemia*, *Hieracium*, *Antennaria*, and *Taraxacum*, the last six being

[1] However, male parthenogenesis has been reported in the brown alga, *Ectocarpus siliculosus*, though here the sperms are relatively large and the plants into which they develop relatively small.

seed plants, and the final three being Compositae. In these cases also parthenogenesis undoubtedly involves the loss of a character formerly present; in *Wikstroemia* and *Hieracium* the pollen often is imperfectly formed or impotent. Parthenogenesis occurs in many animals, as in rotifers and in a number of insects and crustaceans. Like apogamy, parthenogenesis is advantageous in that it eliminates the disadvantages of alternating generations. The elimination of sexual fusion, though often regarded as a sign of degeneracy, is quite as likely to be a sign of progressive evolution. Furthermore, the theory which holds that sexuality leads to variability has little support from the facts of parthenogenesis, since no plant genera are more variable than are *Taraxacum* and *Hieracium*.

Concluding remarks. — So far, at any rate, as the seedless plants are concerned, the significance of sexual reproduction is in doubt, as has been indicated in the preceding paragraphs. The obvious advantages appear to be subsidiary, and not at all commensurate with the amount of energy and material that is involved. The appearance of dioecism, together with that of alternating generations and of heterospory, multiplies disadvantages and introduces no conspicuous corresponding advantages, unless it should be discovered that amphimixis is inherently advantageous; in this event dioecism, alternating generations, and heterospory are highly beneficial, since they increase the chance of fusion between gametes that differ in immediate ancestry. In the seed plants, through the marked subordination of the gametophytic generation, through the retention of the megaspore, and through the dispersal of the embryo (seed), the chief disadvantages of alternation and heterospory are eliminated. To a small extent the disadvantages of alternation are eliminated through apogamy, apospory and parthenogenesis, but the elimination of disadvantage has come chiefly through vegetative reproduction, which in the great majority of plants insures the perpetuation of species, regardless of the presence or absence of sexual reproduction. The almost unlimited capacity for vegetative reproduction in the gametophyte generation of bryophytes and of the sporophyte generation of ferns and seed plants doubtless has been the means of preserving many species that otherwise would have perished. Thus it is not to be assumed that the progress of evolution necessarily is advantageous, and that heterospory and alternation must be an improvement over homospory and lack of alternation. Probably the decadence of the heterosporous pteridophytes and of

many groups of animals is due to disadvantageous trends in evolution. Even in the seed plants, supremacy is due, not so much, probably, to heterospory and alternation, as to various features which eliminate their disadvantages and most of all to their high capacity for vegetative reproduction, for foliage display, and for the development of secondary wood.

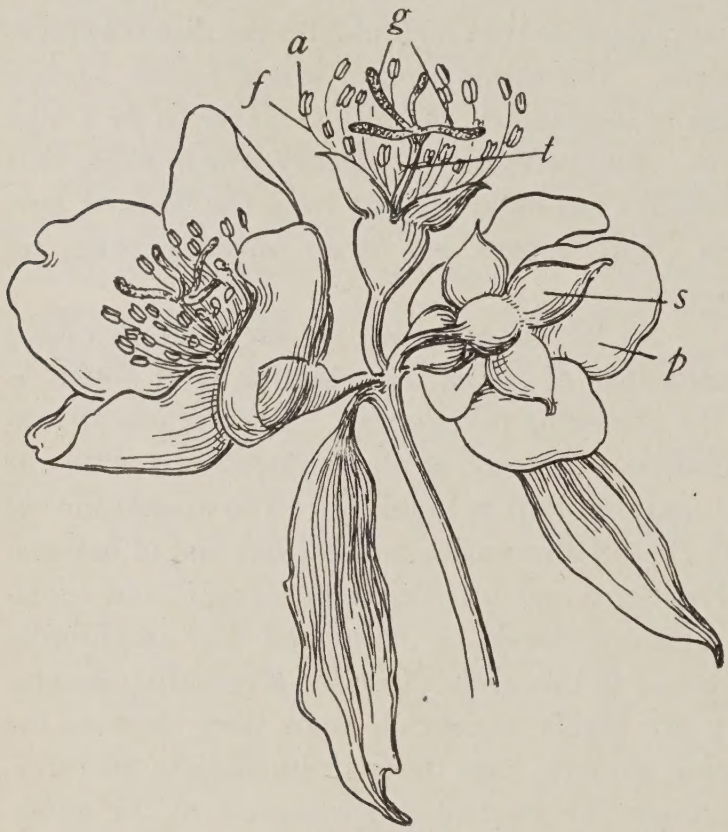


FIG. 442. — An inflorescence of a syringa (*Philadelphus*), showing the floral organs of a hypogynous, monoclinous, polypetalous flower; note the calyx with its individual sepals (*s*) and the corolla with its individual petals (*p*), the calyx and corolla together forming the perianth; note also the stamens, each composed of a filament (*f*) and an anther (*a*), and the pistil, of which there are here to be seen the style (*t*) and four stigmas (*g*); this inflorescence is a cyme, the terminal flower blossoming first.

2. FLOWERS

General characteristics of flowers. — *The parts of a representative flower.* — Ecologically speaking, a *flower* is an organ whose rôle is pollination, which is the initial process of seed production. Structurally, a flower is a shortened shoot with spore-bearing organs, which usually (though not necessarily) are subtended by one or more leaflike structures.[1] In a representative flower the outermost whorl of floral leaves is known as the *calyx*, the individual leaves being termed *sepals* (*s*, *k*, figs. 442, 443). Next within this is the *corolla*, which may or may not be made up of separate leaves, known as *petals* (*p*, *c*, figs. 442, 443). The calyx and

[1] The latter statement groups the strobilar organs of many pteridophytes with flowers, there being no sharp line structurally between strobili and certain floral shoots or inflorescences; however, since the rôle of gymnosperm and pteridophyte strobili is fundamentally different, in the following pages gymnosperms, but not pteridophytes, will be regarded as true flower-producing plants.

corolla together form the *perianth.* Next within the corolla are the *stamens*, each of which consists usually of a slender stalk, the *filament* (*f*, fig. 442), and a spore-bearing body, the *anther* (*a*, figs. 442, 443), the spores being known as microspores (fig. 451). At the center of the flower is the *pistil* (or pistils); a simple pistil or one member of a compound pistil is called a *carpel* (*g*, fig. 443). Commonly a pistil is composed of an enlarged basal portion, the *ovary* (*o*, figs. 486, 487), and a slender upper portion, the *style* (*t*, fig. 442), which is surmounted by the somewhat enlarged and sticky *stigma* (or stigmas, *g*, fig. 442).

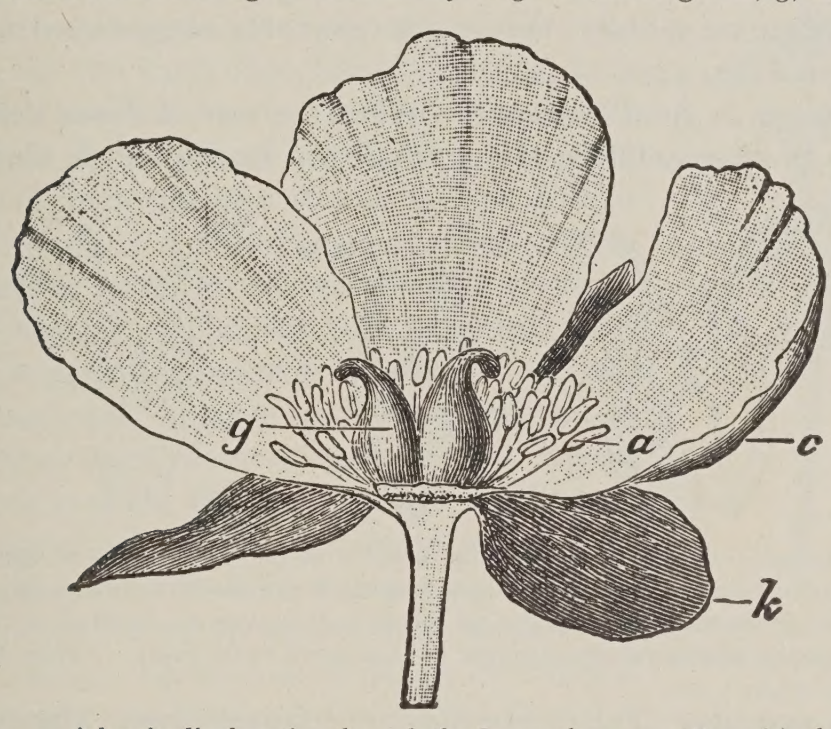


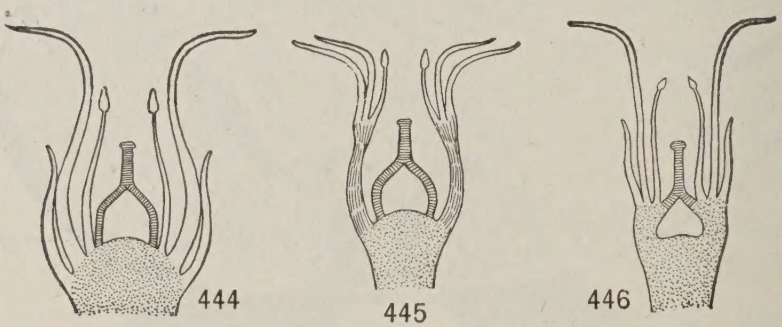
FIG. 443. — A longitudinal section through the flower of a peony (*Paeonia*), showing the calyx with its sepals (*k*), the corolla with its petals (*c*), numerous stamens with their filaments and anthers (*a*), and the pistils or carpels (*g*); the broadened end of the axis just below the carpels is the receptacle. — From STRASBURGER.

Inside of the ovary are *ovules*, which represent incipient seeds, and within each ovule is the megaspore or *embryo sac*, which develops into the minute female gametophyte that is characteristic of seed plants. The entire life of the female gametophyte is passed within the ovule, and after the fusion of the gametes, the sexually produced spore (oospore) germinates into the *embryo*, whose subsequent development is the most conspicuous feature of seed formation. Usually the minute male gametophyte begins to develop from the microspore within the anther, forming a structure of two or more cells which with the persisting microspore wall forms the mature *pollen grain* (fig. 452). The

pollen grains, lodging upon the stigma, germinate, developing elongated structures, known as *pollen tubes*, which penetrate the pistil to the female gametophyte, thus permitting the migrating male cells to reach the neighborhood of the egg.

The more or less broadened terminal part of the axis, which bears the floral organs, is the *receptacle* (fig. 443). Most flowers are subtended by leaflike organs, known as *bracts* (*b*, fig. 447), into which foliage leaves often grade imperceptibly; a group of whorled or closely arranged bracts is called an *involucre* (figs. 499, 500). Although flowers often are solitary, they more commonly are grouped into an *inflorescence* (fig. 447).

Differences in floral structure. — While the sort of flower described above is as representative as any, there are divergences in almost all



FIGS. 444–446. — Diagrams showing the position of the floral organs in hypogynous (444), perigynous (445), and epigynous (446) flowers; in 444 the calyx, corolla, and stamens are attached to the receptacle; in 445 the corolla and stamens are attached to the calyx tube; in 446 the other floral organs appear to be attached to the ovary. — From GANONG.

respects, and since these divergences are relatively fixed, whatever the environmental conditions, they have been made the chief basis for separating seed plants into subdivisions. The kind of flower that is most fundamentally different from the one above pictured is that of the gymnosperms, which has no ovary, style, or stigma, the ovules being exposed directly to falling pollen. Any one of the parts of a flower may be wanting or even all the parts except either stamens or pistils. Often there is but one kind of floral leaves which in the dicotyls is arbitrarily regarded as the calyx (figs. 465, 466), but which in the monocotyls is termed the perianth; sometimes there are no floral leaves, as in the cattails, peppers, and hazels (fig. 467), and in most gymnosperms.[1] Even where the perianth is lacking, one or more bracts commonly are present.

[1] Spikes or catkins of such flowers do not differ essentially in structure from pteridophyte strobili, though their rôle is radically different.

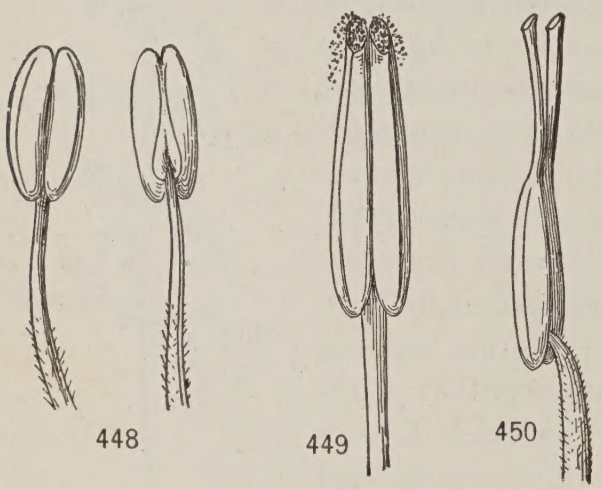
The simplest flower is that of the duckweeds, in which the only organ present is a single stamen or pistil. In the dicotyls the corolla may be made up of separate petals (figs. 442, 443), or the parts may be united (as in the Sympetalae, fig. 491). Most flowers are *monoclinous*, that is, with pistils and stamens occurring in the same flower (figs. 442, 443), but some are *diclinous*, that is, with stamens and pistils occurring in separate flowers; diclinous species may be *monoecious*, having the two kinds of flowers on the same plant (fig. 467), or *dioecious*, having the two kinds on separate plants (fig. 471).

While the floral whorls commonly are sharply delimited, the calyx and corolla often are much alike, as in many monocotyls and in some dicotyls (*e.g. Polygala*). A striking instance of intergrading parts is found in the white water lily (*Castalia*), where the stamens pass gradually into petals, suggesting to some observers that stamens are transformed petals and to others that petals are transformed stamens, neither view having adequate support. When the calyx, corolla, and stamens are inserted on the receptacle below the ovary, the flower is called *hypogynous* (figs. 443, 444); when the corolla and stamens are inserted on the calyx at the level of the ovary, the flower is called *perigynous* (fig. 445); and when the calyx appears to be inserted on the ovary, the flower is called *epigynous* (fig. 446). A *determinate* inflorescence is one in which the terminal flower blossoms first, while an *indeterminate* inflorescence is one in which the lateral flowers blossom first, so that a shoot may continue to bloom somewhat indefinitely (fig. 447). *Cymes* are a representative form of determinate inflorescence (fig. 442), and common forms of indeterminate inflorescences are *spikes* (fig. 469), *catkins* (fig. 467), *racemes* (fig. 505), *corymbs* (fig. 479), *umbels* (figs. 502, 503), *panicles* (fig. 468), and *heads* (fig. 499).

FIG. 447. — A compound raceme of *Coleus*, the individual flowers being arranged in paired cymes; *c*, calyx; *c'*, the sympetalous bilabiate corolla, composed of an ascending upper lip (*v*) and a boat-shaped lower lip (*l*); note the partially exserted stamens (*a*) and style (*t*); the developing cymes are subtended by caducous bracts (*b*).

The significance of differences in floral structure. — The floral divergences heretofore noted are of great convenience in classification,

because they are relatively invariable, but they appear to have had little or no significance in determining the success or failure of plants. It is believed, for example, that the trend of plant evolution has been toward epigyny, but there is practically no evidence that epigyny is more advantageous than hypogyny. Monocliny or dicliny and the presence or absence of a perianth may be of greater consequence, and they will be considered later, but it appears that floral evolution has taken place in large part without relation to rôle or to ecological advantage, especially in those structures most used in classification. In many other respects, however, flowers possess conspicuous advantages, and these will now be considered.

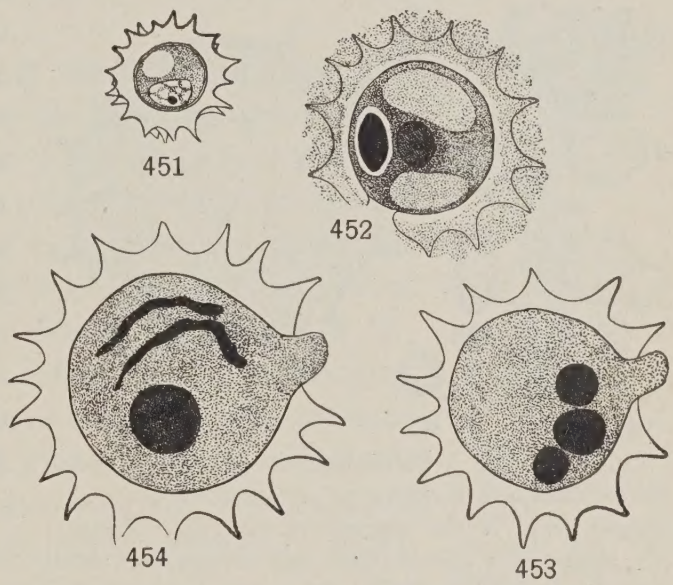


FIGS. 448–450. — Stamens of angiosperms, showing methods of anther dehiscence: 448, ordinary stamens with longitudinal dehiscence; 449, a stamen of *Solanum* with dehiscence by a terminal slit or pore; 450, a stamen of *Vaccinium* with tubular prolongations of the pollen sacs. — From KERNER.

The rôle of flowers and the essential organs involved. — *Pollination.* — *Pollination*, that is, the transfer of pollen grains to the stigma (or to the ovule in gymnosperms) is the chief activity associated with flowers. When pollen is transferred from a flower of one plant to a flower of another, the phenomenon is termed *cross pollination* or *xenogamy*, and when pollen is transferred from the anthers to the stigma of the same flower, it is termed *close pollination* or *autogamy*. *Geitonogamy*, in which pollen is transferred from one flower to another on the same plant, is intermediate between xenogamy and autogamy, and often is classed with the former, but in reality it is much closer to the latter. In many species autogamy is the only kind of pollination possible, and in other species (probably a greater number) only xenogamy is possible, but it is probable that in the great majority of plants both autogamy (or geitonogamy) and xenogamy are possible, though usually it is believed that the latter is the more advantageous. In all cases xenogamy is possible only through the action of external agents, of which wind and insects are the most important. In geitonogamy and autogamy (especially the latter) pollination may occur

through the direct contact of anther and stigma, but gravity, wind, and insects often effect autogamy and geitonogamy as well as xenogamy; in some cases insects are as necessary for autogamy as for xenogamy (as in *Yucca*).[1]

The dehiscence of the anthers. — When the pollen grains are mature, the anther dehisces, usually by longitudinal slits (fig. 448), but sometimes by transverse slits, by valves (fig. 482), or by terminal pores (as in *Solanum* and in the Ericaceae, figs. 449, 450). Dehiscence is occasioned by tissue desiccation. Beneath the epidermis is a layer with unequally thickened fibers, in which strains arise when the water content lessens; rupture then occurs along the lines (or at the spots) of weakness, whereupon the pollen may be shaken out by such agents as wind and insects.

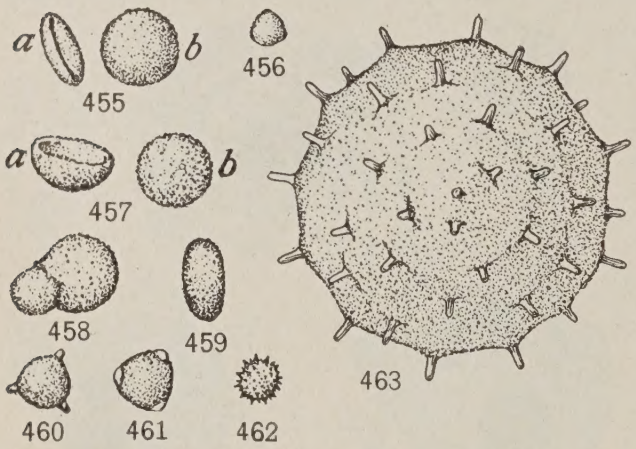


FIGS. 451–454. — Different stages of pollen grain development in a rosin-weed (*Silphium*): 451, a microspore, representing the one-celled stage of a developing pollen grain; 452, a mature pollen grain; 453, 454, germinating pollen grains, showing the first stages of pollen tube development; note the thick and spiny outer coat (exine); highly magnified. — From MERRELL.

The pollen. — The pollen grains are borne in *pollen sacs* within the anther, where they commonly are produced in fours (*tetrads*). Usually the grains break apart at maturity, scattering independently, but in some plants they cohere in groups (as in *Mimosa*), while in others they cohere in large and definite masses, known as *pollinia* (as in the milkweeds and the orchids). Pollen grains commonly have a thick outer layer, the *exine*, and a delicate inner layer, the *intine* (figs. 451–454); in cases where there is a single layer, it may be thick and cutinized (as in *Senecio*) or thin and permeable (as in submersed aquatics). Pollen grains differ considerably in shape, the common forms being spherical or ellipsoidal (figs. 455–463), and also in size, those of some mallows

[1] On this account the term *self-pollination*, if used, should be restricted to contact pollination, rather than be made synonymous with autogamy in general.

being a hundred times as large as the grains of many other plants (fig. 463); they differ also in surface sculpturing, most grains being smooth, but some being spiny, as in the composites and the mallows (figs. 462, 463). Many pollen grains have thin spots which upon germination determine the position of the developing pollen tubes; in some cases the tube forces off a part of the spore coat as a lid. The cutinized outer coats of pollen grains are so resistant to decay that they are recognizable in peat and lake deposits thousands of years old. The pollen of different tree species recovered from such peat and lake deposits when counted, analyzed, and arranged according to the relative abundance of the species has been of great service in assisting in the reconstruction of climatic and vegetational changes that have occurred in Europe and America since the last glacial period, a period of some 15,000 years or more.



FIGS. 455–463. — Pollen grains; 455, grains of *Euphorbia splendens*, both dry (*a*) and moistened (*b*); 456, angular grain of the nightshade (*Solanum nigrum*); 457, grains of a croton (*Codiaeum variegatum*), both dry (*a*) and moistened (*b*); 458, a germinating pollen grain of *Oxalis*; 459, ellipsoid grain of *Impatiens sultani*; 460, grain of *Cuphea ignea* with processes at the angles; 461, grain of a nasturtium (*Tropaeolum*) with prominent angles; 462, spiny pollen grain of *Bidens*; 463, grain of *Hibiscus* with prominent spiny processes; note the relatively gigantic size; all equally magnified.

The stigma. — The essential elements of the pistil are the ovary and the stigma, the style often being short or wanting, though its presence may be advantageous through its elevation of the stigma into a region of optimum exposure to pollen. When mature, the stigma secretes mucilaginous substances, which, together with its papillate or spinescent surface, facilitate the adherence of pollen (fig. 464). Stigmas also secrete substances which facilitate the germination of pollen grains, and in some cases they secrete very specialized substances which stimulate the germination of pollen from flowers of the same or nearly related species, but which have either no effect or a detrimental effect upon other pollen.

The pollen tube. — Under suitable conditions pollen grains adherent to the stigmatic surface germinate, and the developing pollen tube,

which is the bearer of the male cells, penetrates the style and enters the ovary; ultimately it may reach the female gametophyte inside an ovule, where the fusion of the gametes takes place. Usually the pollen tube enters the ovule through the *micropyle*, which is a narrow channel at the ovule apex where the enveloping integuments have not quite grown together. In some species the pollen tube penetrates the pistil so rapidly that the gametes fuse a few hours after pollination, while in other species a number of months elapse between pollination and gamete fusion (as in the oaks and pines).

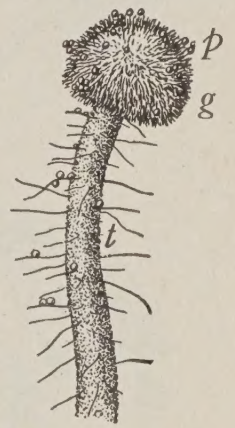
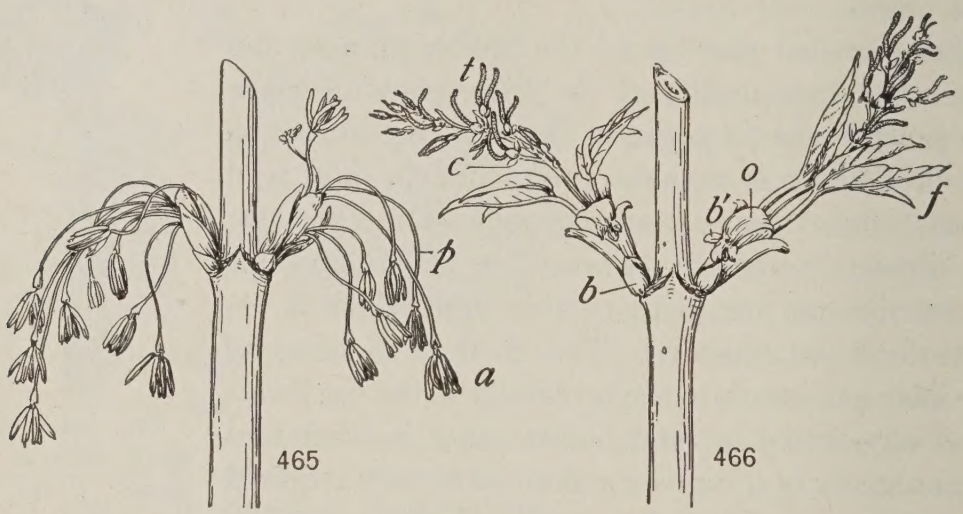


FIG. 464. — Stigmatic region of *Hibiscus; t*, the upper part of a style branch with scattered hairs; *g*, the stigma with its hairy surface to which pollen grains (*p*) are adhering; highly magnified.

The secluded position of the female gamete and the usual non-motility of the male gametes make the pollen tube an organ of the first importance in the facilitation of sexual reproduction in most seed plants, since it bears the male cells (sometimes for an almost incredible distance) in its fungus-like course through the pistil tissues, from which it derives food parasitically. This method of bringing the male gametes into the proximity of the egg seems especially suited to land plants, since it eliminates the necessity of a liquid medium, such as is required by motile sperms. Pollen grains germinate readily in various liquid media, swelling rapidly and sending out tubes for a short distance. In respect to conditions favoring germination, pollen grains show wide diversity, especially in their osmotic relations with the medium. The pollen of a number of species germinates readily in distilled water, but in other cases this medium causes the grains to burst; *Canna* grains, for example, burst in water, but not in a 2 per cent cane sugar solution. Most pollen germinates in cane sugar solutions, that of some species requiring high concentration, while that of others germinates readily in solutions of low concentration. Pollen grains that are difficult to germinate (as those of the grasses) send out tubes if they absorb water slowly. Some pollen (as in certain umbellifers and composites) has never been seen to germinate except on stigmas. Probably because of the presence of the proper stimulating substance at the proper degree of concentration, germination usually takes place more readily on stigmas than in artificial media, and com-

plete development does not occur unless germination has taken place on the stigma of the proper plant (*viz.* of the same or of a closely related species) [1]; in some species pollen is essentially impotent on the stigma of the flower in which it was produced (p. 370). Pollen grains usually retain their vitality for a number of days, but those of *Hibiscus trionum* live scarcely more than three days, while those of some species (as the date palm) may live for several months, especially if kept dry. Usually pollen grains that have been moistened and subsequently dried die quickly, but some pollen is so resistant that submergence for a num-



FIGS. 465, 466. — The dioecious wind-pollinated flowers of the box elder (*Acer negundo*): 465, fascicles of drooping staminate flowers borne on long stalks or pedicels (*p*); note the prominent anthers (*a*); 466, ascending racemes of pistillate flowers from another tree; note the perianth, consisting only of a calyx (*c*), and also the two prominent stigmas (*t*); note also the transition between the bud scales (*b*) and the ordinary foliage leaves (*f*), the intermediate leaves having a prominent flattish petiole (*o*) and a small trifoliate blade (*b'*).

ber of hours does not impair its vitality. The pollen of vernal flowers is especially resistant, not only to moisture, but also to low temperatures. In general, the stigmas are more sensitive to harmful factors than are the pollen grains.

Pollen tubes usually take a more or less direct course toward the ovary. Commonly the central region of the style is composed of delicate elongated cells, or sometimes, even, it is hollow, so that the direct course is the easiest; in the grasses, however, the region

[1] Often germination, but not the later stages of development, may take place on the stigmas of unrelated plants; the pollen tubes of *Ranunculus*, a dicotyl, have been seen penetrating to the micropyle of *Scilla* a monocotyl. It may be noted in this connection that the sperms of ferns swim into the archegonia of many species indifferently, but that fusion with the egg takes place only in the same or in a closely related species.

traversed by the pollen tube seems no more easily penetrable than do the adjoining tissues. After leaving the style and entering the ovary, the pollen tube commonly follows the inner wall, and it may pursue a tortuous course, or it may grow directly toward a micropyle; pollen tubes have been shown to exhibit prochemotropic reactions toward certain carbohydrates and proteins, including those that are secreted by stigmas.

Wind pollination. — *Features that favor the scattering of pollen.* — The simplest form of pollination and the one most closely related to spore dispersal in the lower plants is *wind pollination*,[1] and wind-pollinated plants have many features which resemble those of the fungi, bryophytes, and pteridophytes rather more than they do those of the insect-pollinated seed plants. In many cases the staminate flowers are arranged in *catkins*, which usually are slender, pendulous inflorescences that yield gracefully to breezes (fig. 467). Catkins suited for wind pollination are especially characteristic of many trees and shrubs (notably the poplars, oaks, birches, and other Amentiferae, and also most of the conifers), which perhaps is advantageous in view of the relative exposure of such plants to wind; in most of these plants, also, the flowers develop before the leaves, thus further facilitating exposure to wind. The pistillate flowers sometimes are in catkins (as in poplars and birches), but often they are not (as in oaks and hickories); such arrangement. apparently, is of no particular advantage.

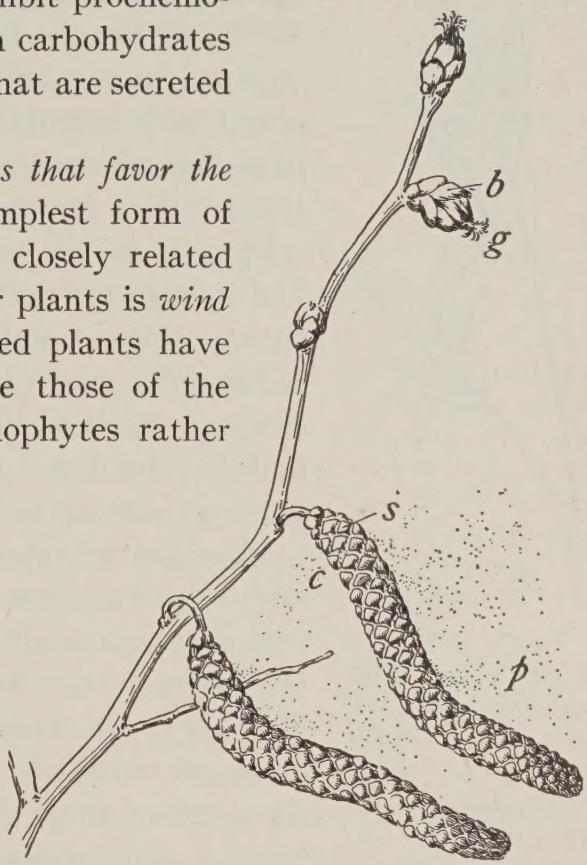


FIG. 467. — A flowering twig of a hazel (*Corylus americana*), a shrub which has monoecious wind-pollinated flowers; note that the staminate flowers are lowermost and are in catkins (*c*) which sway in the breeze, the pollen grains (*p*) often appearing in clouds; *s*, scale leaves which protect the flower buds in winter; the pistillate flowers develop from scaly buds (*b*), and at anthesis the stigmas (*g*) are exserted.

[1] Species with wind pollination often are called *anemophilous*, a term that should be discarded, together with other humanistic words as applied to plants.

In many species with wind pollination, and especially in those without catkins that move readily in the wind, the stamens have long and slender filaments, which so expose the anthers that they are shaken in the gentlest air movements (as in the grasses and the box elder, figs. 465, 468, 469). In the nettles the pollen is discharged into the air by a sudden movement of the filaments. In many plants pollen that falls in quiet weather accumulates in pockets of one sort or another, whence it is scattered readily by the first breeze. In most wind-pollinated species (not, however, in most grasses and sedges) the pollen is produced in great abundance; this is a matter of much advantage in view of the great waste. The abundance of pine pollen results sometimes in the so-called sulphur showers, and the abundance of ragweed pollen in the air is a factor in causing hay fever.

FIG. 468. — A panicle branch of the meadow fescue (*Festuca elatior*), a plant with monoclinous wind-pollinated flowers; note the unopened spikelets above with their imbricated scales; below to the right is a spikelet in which two of the lower flowers have opened, each disclosing two plumose stigmas and three stamens whose long and slender filaments expose the anthers to the wind.

Wind-scattered pollen commonly is smooth, light, and dry, and hence easily blown about (fig. 467), and in the pines, dispersal is facilitated further by the presence of a wing on each side of the grain (fig. 470). In wind-pollinated species the pollen grains are not easily wetted, thus further resembling the spores of fungi and ferns; this is highly advantageous, since moistening might prevent wind dispersal and lead to premature germination. Even among the submersed aquatics there are some species (*e.g.* many pondweeds) that at anthesis develop aerial flowering shoots, which produce light pollen that is not easily wetted and that is scattered by wind.[1] The fact that anthers dehisce chiefly when dry is of much significance in the protection of pollen from moisture.

Features that favor pollen reception. — In wind-pollinated species the stigmas commonly are large and conspicuously exserted (figs. 466, 467), and sometimes they are feathery plumose (as in the grasses, figs. 468, 469), the " silk " of corn

[1] This phenomenon is especially striking in *Myriophyllum*, since the hitherto flaccid and submersed main stem axis becomes at the tip rigidly erect and emersed just before anthesis.

being a familiar and conspicuous example of these characters. In the conifers, where there is no stigma, the pollen may be caught in a drop of mucilaginous liquid exuded from the ovule.

Features that favor cross pollination. — While wind-pollinated flowers structurally are relatively simple, they are on the whole as well fitted for cross pollination as are insect-pollinated species, and they exhibit even many of the specialized features which are regarded as more characteristic of the latter. In the first place, many and perhaps most wind-pollinated plants are diclinous, and in these, of course, there can be no autogamy. A large number of the diclinous forms are dioecious (*e.g.* the poplar, ash, box elder, juniper, date palm, and meadow rue), and their pollination necessarily is xenogamous (figs. 465, 466). Among common monoecious forms are the oaks, hickories, birches, alders, pines, nettles, and most of the sedges (fig. 467); while geitonogamy as well as xenogamy might occur in such plants, the chance of it is minimized in the many cases in which the pistillate flowers are higher than the staminate (as in the hazel, the pine, and in many sedges). Furthermore, in many monoecious species the pistillate flowers of a given individual blossom before the staminate, and sometimes several days before, as in some alders and cattails. Even in dioecious plants the pistillate flowers commonly mature before the staminate.

FIG. 469. — The upper part of a plantain spike (*Plantago*), illustrating protogyny in monoclinous wind-pollinated flowers; note that the conspicuous plumose stigmas (*g*) appear before the stamens are evident; in the older flowers note the long and slender filaments (*f*) and the triangular anthers (*a*); *c*, calyx; *c'*, corolla.

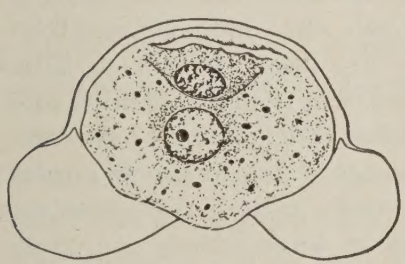


FIG. 470. — A pollen grain of a pine (*Pinus*), showing the two wings which aid in its dispersal by wind; highly magnified. — From COULTER and CHAMBERLAIN.

In monoclinous wind-pollinated flowers (as in the grasses and plantains, figs. 468, 469), cross pollination commonly is favored by the consecutive maturity or *dichogamy* of the anthers and stigmas. In the plantain (fig. 469) the stigmas mature first, exhibiting a phenomenon known as *protogyny*, while the earlier maturation of the anther is known as *protandry;* both protandry and protogyny are seen in maize. The most specialized means of preventing close pollination, namely,

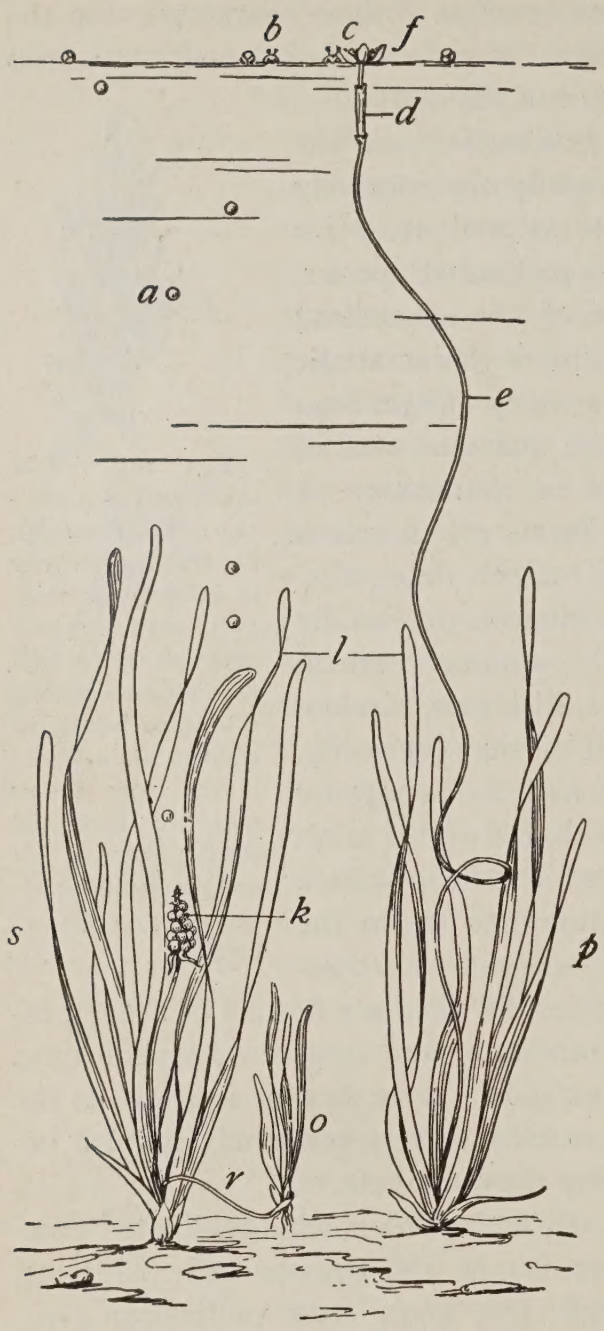


FIG. 471. — Pollination in the tape grass (*Vallisneria spiralis*); *s*, staminate plant; *p*, pistillate plant; the staminate flowers are borne in a spike (*k*); upon detachment they rise (*a*) to the surface, open out (*b*), and float on the water; the pistillate flowers (*f*) are borne in spathes (*d*) on long scapes (*e*), just reaching the water surface, where the floating staminate flowers may come in contact with them (*c*); note also the vertical ribbon-like leaves (*l*) and the stolon (*r*), *o* representing a new potential plant or offset. — After KERNER.

that in which the pollen is impotent on the stigma of the same flower, is illustrated in rye, though in wheat and barley, and probably in most monoclinous species, close-pollination is not excluded.

Miscellaneous features of wind-pollinated flowers. — Wind-pollinated flowers usually contrast with those that are insect-pollinated in their lack of showiness, odor, and nectar, though some of them are conspicuously colored (as in the cottonwood and field sorrel). The perianth mostly is inconspicuous (either through its greenish or brownish color or its small size) and often it is absent; when present, it consists commonly of a calyx, the corolla being rarely in evidence. None of these features would occasion comment, but for the corresponding presence of showiness, odor, and nectar in insect-pollinated flowers and for the consequent assumption that in the latter these features probably are advantageous. The distribution of species with wind-pollinated flowers has been thought to differ somewhat from that of other seed plants. For example, the percentage of the former is greater in windy habitats than elsewhere (as on small islands and along shores), while the flowers of our northern trees contrast with those of tropical trees in being predominantly wind-pollinated.

The advantages and disadvantages of wind pollination. — The question of advan-

tage is here largely one of speculation. Undoubtedly a great disadvantage in wind pollination is the enormous waste of pollen. Probably not more than one out of a thousand or even out of many thousand grains ever reaches the proper stigma. Perhaps, on the other hand, the chance of a favorable wind is greater than that of a visit by the proper insect. The dominance of wind pollination in such plants as the oaks, pines, grasses, and sedges at once suggests that wind pollination certainly is not detrimental. However, the great abundance of such plants (especially the grasses and sedges) is quite as likely to be due to vegetative as to reproductive organs.

Water pollination. — Pollination through the agency of water is a relatively rare occurrence but it is of much interest. In plants that are completely submersed (as in several of the Potamogetonaceae and Najadaceae) the pollen grains are filamentous structures that are as heavy as water or heavier, and the thick exine characteristic of aerial pollen is lacking; such pollen grains upon release float below the surface and may come into contact with the long exserted stigmas.

In the tape grass (*Vallisneria*) and in some of its relatives, pollination takes place at the water surface. *Vallisneria* (fig. 471) is a dioecious plant, whose pistillate flowers are single and are borne on long scapes that bring the flower at the time of stigmatic maturity just to the water level. The staminate inflorescences at maturity become detached from their short scapes and rise to the surface; upon the opening of the bract (*spathe*), the individual flowers also become detached and float about on the water as miniature boats, the perianth opening and exposing the stamens. The floating staminate flowers, like any small particles, swirl readily into the slight depressions formed about the pistillate flowers, as about other objects on the water, and come into contact with the stigma. After pollination the scape of the pistillate flower coils up into a spiral, thus withdrawing the ovary below the surface, where the fruit develops. In essential respects pollination in the water weed (*Elodea*) is comparable to that in *Vallisneria*.

General characteristics of insect-pollinated flowers. — *Monocliny and its advantages.* — Were it not so common, the symbiotic relation existing between flowers and insects would be regarded as most marvelous. From the standpoint of evolution, no great facts of nature are more remarkable than that in many plant species the flowers remain unpollinated unless they are visited by insects in search of nectar or pollen, and that in a much greater number of species visiting insects are the chief agents of pollination. *Insect-pollinated* flowers [1] are in great part monoclinous (figs. 442, 443), though a few are diclinous; for example, the willows are dioecious, and many composites are monoecious. Dicliny has been thought to be advantageous in wind-pol-

[1] Insect-pollinated flowers often are inaptly called *entomophilous*, that is, insect-loving.

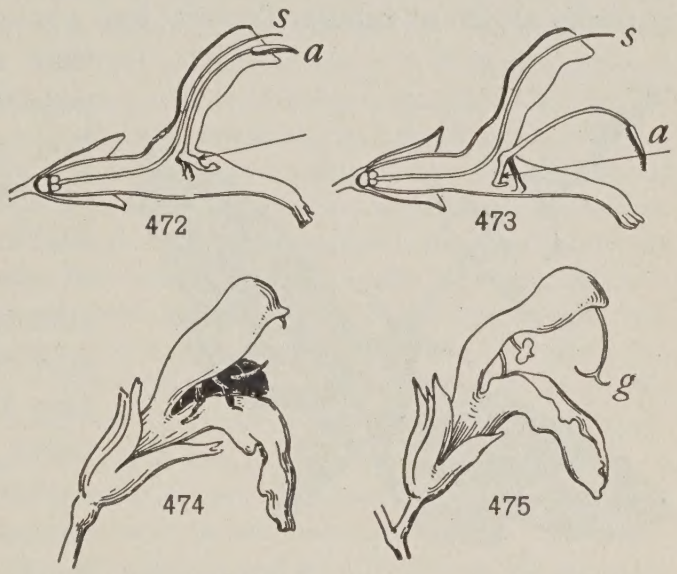
linated flowers because it increases the probability of cross pollination; however this may be, monocliny would seem to have a distinct advantage in insect-pollinated flowers in that it makes possible double the amount of pollination for a given number of insect visits. Furthermore, pollen-gathering insects would not visit pistillate flowers and nectar-gathering insects would visit both pistillate and staminate flowers only in case each were nectar-bearing, thus involving two nectaries in one act of pollination.

Pollen. — The stamens of insect-pollinated flowers rarely are prominently exserted and the filaments often are short; also the inflorescences are relatively inflexible in the wind. The pollen, instead of being dry and powdery, commonly is adhesive through the possession of spines or of other protuberances (figs. 462, 463), or through the presence of viscid substances (as in *Oenothera*), so that the grains often cohere in masses. The shape of the grains is more likely to be elliptical than spherical, the latter shape being especially characteristic of the grains in wind-pollinated flowers. Such pollen grains are not easily blown about by the wind, and they adhere readily to visiting insects and to stigmatic surfaces. In species with wide-open flowers, which therefore are exposed to insects of all kinds, including pollen-gathering insects, the pollen often is almost as abundant as in wind-pollinated species; sometimes also the stamens in such flowers are very numerous (as in the roses and buttercups). In tubular or otherwise partly closed flowers, where the stamens are concealed, the latter commonly are few in number and the pollen is relatively sparse (as in the phloxes and mints). As a rule, the stigmas are smaller and otherwise less conspicuous than in wind-pollinated flowers.

Features supposed to be attractive to insects. — The most noticeable single feature of insect-pollinated flowers is their showiness, which is due to the color of the flowers, or to their size, position, or arrangement. Many insect-pollinated flowers are fragrant, and many also possess nectar. It is rare that a flower which is pollinated regularly by insects is neither showy, fragrant, nor nectar-producing, and some insect-pollinated flowers have all these features.

Most insect-pollinated plants north of the tropics are of low stature, but in warm countries many trees have insect-pollinated flowers. An odd phenomenon, commonest in the humid tropics (but characteristic also of our northern redbud, *Cercis canadensis*), is *cauliflory* (*i.e.* stem flowering), the tree trunks often being covered with flowers; this habit is without obvious advantage, though it has been suggested

that trunk flowers are well protected from torrential rains. Cauliflory appears to be stimulated by an excess of moisture; it has been induced in the grape also by wounding and in the orange by defoliation. In some tropical trees and shrubs (as in *Ficus geocarpa*) flowers break through the soil from subterranean stems. Transitions between wind-pollinated and insect-pollinated flowers sometimes are seen, as in the ericads, where the pollen which commonly is scattered by insects ultimately becomes dry and powdery and thus may be scattered by the wind; chestnut flowers which usually are wind-pollinated are fragrant and attract insects. *Ephedra campylopoda* is interesting as being an insect-pollinated gymnosperm, the flowers, which are much frequented by insects, exhibiting nectar and sticky pollen which coheres in masses. Before considering in detail the features that attract insects to flowers, it is necessary to consider the pollinating organisms themselves.



FIGS. 472–475. — Flowers of *Salvia*, illustrating pollination by bees: 472, a flower of *Salvia glutinosa* in longitudinal section, the arrow indicating the direction taken by visiting bees; *s*, style; *a*, anther; 473, a similar section, showing the lower arm of the connective lever pushed back, as by an entering bee, the pollen-bearing anther (*a*) thus being deflexed in such a way as to rub pollen over the insect; 474, a *Salvia* flower into which a bee has entered, the anther (*a*) being in contact with the bee; 475, an older flower, showing the stigma (*g*) in such a position as to come into contact with an entering bee; 474 and 475 show that *Salvia* is protandrous. — 472 and 473 from KERNER; 474 and 475 from AVEBURY (LUBBOCK)

Pollinating insects. — *General remarks.* — The vast majority of efficient pollinating animals are insects, particularly flying insects, since those which crawl from flower to flower are likely to brush off most of the pollen *en route*. Among the flying insects those that visit flowers regularly for nectar or pollen are the most important. Flowers with exposed nectar and pollen are visited by most of the flower-frequenting species, but flowers with hidden nectar or pollen, especially those with long corolla tubes or whose nectar accumulates in long *spurs* (fig. 477), are pollinated only by highly specialized insects with elongated mouth parts.

Bees. — The most important pollinating insects belong to the Hymenoptera, a group which includes the bees, wasps, and ants. The

honeybee (*Apis*) and the bumblebee (*Bombus*) are the most efficient of all pollinating insects, because of their remarkable and continued activity from the opening to the close of the flowering season, because of their precision, which insures the successive and rapid pollination of many individuals of the same species, and because they visit flowers for pollen as well as for nectar. Their hairy legs are well suited for carrying pollen, and their long *probosces* enable them to secure nectar in partially closed or tubular flowers (figs. 472–475). Among the flowers that are almost entirely dependent upon bees for pollination are those with irregular (*zygomorphic*) corollas, as in the legumes, the violets, and many of the mints; in certain instances (as in the clovers and aconites) the natural distribution area is confined to those parts of the world frequented by bees. The bees are diurnal insects and visit only diurnal flowers, and it commonly is thought that they have a high color sense and a keen sense of smell which aid them in detecting the presence of flowers. The wasps are of minor importance as pollinating insects, though some flowers are pollinated chiefly by them (as in the figwort).

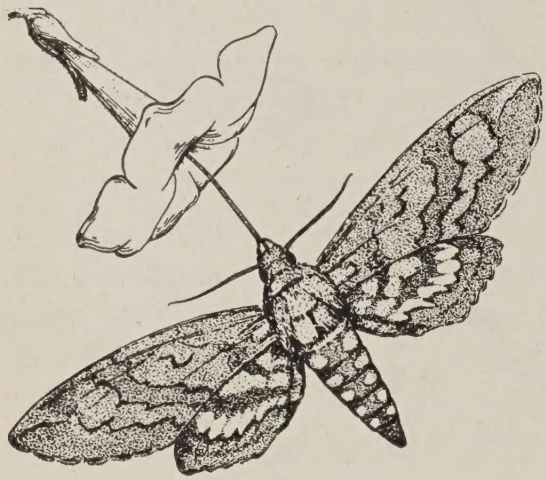


FIG. 476. — A hawk moth (*Phlegethonius sexta*) visiting the flower of *Petunia;* note the long corolla tube of the flower and the long mouth parts of the insect. — After FOLSOM.

Moths and butterflies. — The butterflies and certain moths (classed in the Lepidoptera) are nectar-feeders, and they possess greatly elongated and specialized mouth parts, known as *maxillary laminae.* The butterflies, like the bees, are diurnal insects and are able to get nectar from deeply hidden parts of the flower; as a rule, they visit showy and fragrant flowers (such as various honeysuckles and pinks). Most remarkable, perhaps, are the hawk moths (Sphingidae), a group consisting chiefly of nocturnal insects with maxillary laminae of great length (up to 80 mm.), which are coiled when not in use (fig. 476). The nocturnal hawk moths visit flowers rapidly and with the precision of bees, thus contrasting with the more languid and haphazard movements of the butterflies; they are attracted especially to heavily

scented white nocturnal flowers with long corolla tubes (*e.g. Nicotiana alata*, which becomes fragrant as it opens in the dark).

Flies and beetles. — As a class the flies (Diptera) are not very important pollinating insects, largely because of their absence of precision in making floral visits. Some, however, notably the drone flies (Syrphidae), have extended probosces and depend largely upon flowers for food, and thus are important pollinating agents. Most flies pollinate only flowers with exposed nectar and pollen (as in *Evonymus*). Color seems to have but little attractive significance, but odors (especially those offensive to human nostrils) attract numerous flies, particularly carrion flies and dung flies, which may thus be important pollinating agents in ill-smelling flowers like *Rafflesia*. The pollination of *Arum* and *Aristolochia* is thought to be effected largely by small flies, which are able to crawl through the narrow apertures. Beetles are still less important than flies, though some species with narrow elongated heads are of some significance; as a class their floral visits result in more harm than benefit.

Pollinating animals other than insects. — Apart from insects the most important pollinating animals are birds, especially those with long slender bills and protrusile tongues, such as the humming birds, which visit honeysuckles, trumpet flowers, and other long-tubed blossoms containing nectar; in some cases birds visit flowers in search of nectar-feeding insects. Bird pollination is much commoner in the tropics and in the southern hemisphere than in northern latitudes; in parts of South America, humming birds almost equal insects in importance as pollinating agents, and in South Africa the sunbirds and their relatives are even more important, pollinating insects being much less conspicuous than in the northern hemisphere. The structure of bird-pollinated flowers does not differ from that of flowers which are pollinated by insects with elongated mouth parts. A few instances of pollination by bats have been reported, but they are not regarded as important. Pollination by slugs or snails is of possible importance in a few cases, as in *Calla* and in other aroids with numerous blossoms close together near the ground.

The food of pollinating insects. — *Pollen.* — Pollinating insects visit flowers to obtain pollen, nectar, or sap, and sometimes for shelter, and it is while they are engaged in one or more of these activities that pollination takes place incidentally. Bees obtain nectar, which they store for future use, and pollen, which is in large part utilized more immediately by the larvae, while butterflies and moths obtain only nectar and that for immediate use; it is largely because of this that the bees are more useful pollinators than are the more highly specialized butterflies. In some flowers there is little or no nectar (as in *Papaver*, *Hypericum*, and *Solanum*) and insect visits are made mainly for pollen, which usually is produced in considerable abundance. The insects presumably get most of the pollen, but some of it is pretty certain to be rubbed off on the stigmas. Nectarless insect-pollinated flowers commonly are regular (*actinomorphic*) and wide open, with the anthers

prominently exposed. Sometimes there are two kinds of stamens (as in *Cassia*), one which the insects visit for pollen and another which sprinkles pollen over the insects in such a way that it is likely to come into contact with the stigmas.[1] Commonly pollen-gathering insects are relatively non-specialized (except in the case of bees), corresponding in general to the lack of specialization in the flowers, in which the pollen is so exposed that it may be taken readily by any insect that visits it.

Nectaries and nectar. — Nectar-secreting flowers commonly are more specialized than are nectarless flowers, and the nectar-gathering insects are the most specialized of pollinating insects. However, there are many simple actinomorphic flowers with exposed nectar (notably among the umbellifers) or with nectar but slightly concealed (as in the crucifers), which are frequented by flies and by other insects with short probosces. From these simple nectar-producing flowers there are gradations in the degree of concealment of nectar to the highly specialized and often zygomorphic forms in which it is concealed at a considerable depth at the base of long corolla tubes or in elongated spurs (fig. 477), where as a rule only the most specialized insects with long mouth parts can obtain it. In most cases it is difficult or even impossible for insects getting the nectar to avoid rubbing against anthers and stigmas, thus facilitating pollination. As a rule, the pollen in nectar-bearing flowers is not abundant, and in long-tubed and zygomorphic flowers it commonly is concealed.

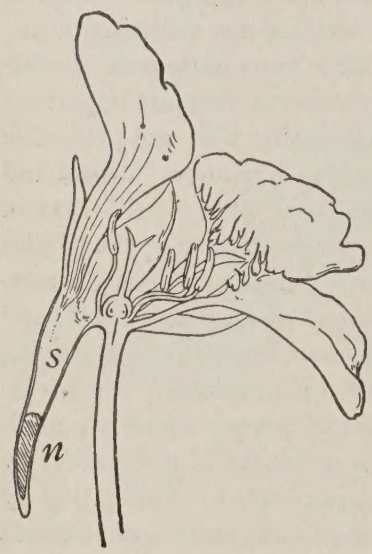


FIG. 477. — A longitudinal section through a nasturtium flower (*Tropaeolum majus*) showing the spurs (*s*) with nectar (*n*) collected in its lower portion; this flower is hypogynous and zygomorphic. — From BARNES.

Most arctic and alpine flowers and also most vernal flowers of temperate climates are comparatively simple in structure and have their nectar supply relatively exposed. On the other hand, many tropical flowers and a large number of estival flowers of temperate climates have more specialized structures, their nectar supply

[1] The high degree of specialization here present is shown by the fact that the pollen which is used for food does not readily germinate on account of the absence of the proper enzyme; when this is supplied artificially, it germinates as readily as does the pollen from the other stamens.

being hidden in spurs or at the base of long corolla tubes. With the former there may be associated the general prevalence of insects with short probosces, characterizing climates or seasons of low temperature, and with the latter there may be associated the more specialized estival or tropical insects with long probosces. The attraction of pollinating insects is not the only advantage derived from floral nectar; there has been previously noted the possibility that nectar associated with the stamens may withdraw water from anthers, causing their dehiscence. It has been suggested also that nectar may play some part in the maturation of fruit, and that it may help to protect flowers from desiccation; the last-named rôle seems especially evident in the case of flowers with water calyxes.

Nectar is secreted by special structures, known as *nectaries*, and there exist all gradations between those which are composed of undifferentiated nectar-secreting tissue and those which are specialized glandular hairs of complex structure. Usually they are associated with the corolla, but they may be connected with the stamens or with any other floral part, even with the involucre (as in the poinsettia, *Euphorbia pulcherrima*), or they may occur on vegetative organs, where they are called *extrafloral nectaries* (p. 373); in the poinsettia, insects may get the abundant nectar without pollinating the flowers, and in the case of the extrafloral nectaries the visitors rarely are efficient pollinating agents. The secreting regions are composed of epidermal cells rich in cytoplasm; commonly they are long and narrow and closely packed in palisade-like rows (fig. 478). Nectaries differ from other glands chiefly in secreting sugar; the process is not well understood, although the presence of sugar outside the cell causes the withdrawal of water from within and the consequent formation of a drop of nectar, of which sixty to eighty-five per cent usually is water. Sometimes the nectar forms in sufficient quantity to drip from the secreting surface, and in some such cases it collects in protected pouches or sacs, which usually are corolla structures known as *spurs* (fig. 477). In most cases the secretion of nectar occurs only at anthesis, though it may continue for some time after pollination, as in the tulip and the quince. The secretion of water, but not of sugar, is greater in humid than in dry weather, quite as with hydathodes. Indeed, there exist all gradations between nectaries and hydathodes. Especially interesting transitional

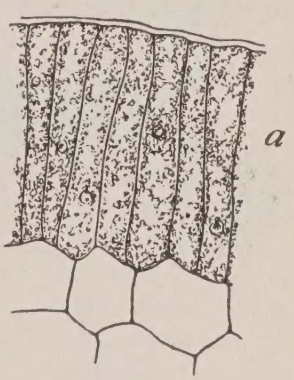


FIG. 478. — A longitudinal section through a floral nectary of the poinsettia (*Euphorbia pulcherrima*), showing palisade-like secretory cells (*a*) which are rich in cytoplasm; highly magnified.

forms are seen in certain tropical flowers, whose glandular hairs secrete but little sugar though exuding large quantities of water, which accumulates in the outer floral organs, giving rise to the term *water calyx.*

In a few cases insects visit flowers for other kinds of food than pollen or nectar, as in certain orchids (*e.g. Maxillaria*), where there occur on the lip of the corolla fragrant hairs rich in fatty and albuminous foods. Some flowers and inflorescences develop a considerable degree of heat at anthesis, and it has been claimed that certain insects visit them for nocturnal shelter and warmth. Since most of the conspicuous heat-producing flowers and inflorescences are found among tropical palms and aroids, this view seems untenable.

Floral features accessory to pollination. — *Color.* — The rôle of the pistil and the stamens is very obvious; the protective and synthetic rôle of the calyx also is obvious (p. 385), but the rôle of the corolla is far less evident. The corollas of flowers, taken as a whole, are ephemeral organs whose evanescence is due to their extreme delicacy and consequent easy wilting, and to their early abscission, much after the manner of deciduous foliage leaves. Corollas present a most bewildering luxuriance of form, color, and marking without parallel elsewhere among plant organs. Most colors except black and green occur commonly, and flowers therefore contrast sharply with the foliage. Reds and blue are due to anthocyanins dissolved in the cell sap, the former indicating maximum acidity and the latter minimum acidity; indeed, certain flowers, as in *Lychnis*, vary in color with the varying acidity of the cell sap. Some yellow flowers owe their color to pigments related to the anthocyanins and like them dissolved in the cell sap. Orange colors and many yellow colors are due to plastids colored with carotin, xanthophyll or with related pigments (fig. 56). Brown colors are due commonly to a combination of plastid and sap pigments. Flower pigments are believed to be oxidation products, and whiteness, which denotes the absence of pigment, arises where the necessary oxidizing ferment (oxidase) is absent, or, if present, is neutralized by reducing agents. The peculiar color-like effect of white flowers is due to the presence of air in the petals or to unequal reflection and refraction. Nocturnal flowers

FIG. 479.—A flowering shoot of the yarrow (*Achillea millefolium*), illustrating the massing of flowers into heads (*h*), and the massing of heads into a compact corymb; *r*, ray flowers; *i*, involucre.

especially are likely to be white, and many species, whose flowers commonly vary from blue to red, may produce white sports, known as *albinos*. The more or less fundamental distinction between the anthocyanin (or *cyanic*) flowers and the yellow (or *xanthic*) flowers is shown by the fact that species and even genera rarely change from one to the other; for example, hepaticas and asters, with all their variations, are not yellow, or goldenrods and sunflowers cyanic. The cyanic colors would seem to be the more specialized, since they contrast more sharply with the foliage, not only in aspect but fundamentally, inasmuch as most yellow petals resemble foliage leaves in having plastids.

FIG. 480. — Flowers of *Coleus*, illustrating zygomorphy; the calyx (*c*) and the sympetalous corolla (*c'*) are bilabiate, the latter having an ascending upper lobe (*b*) and a descending boat-shaped lower lobe (*a*), from which the stamens and the style are partially exserted; the lower lobe of one flower (*f*) is held to one side, so as to show more clearly the upturned style (*t*) with its two-lobed stigma (*g*) and the four stamens (*s*).

In many flowers showiness is increased by the presence of party-colored effects. Sometimes the two halves or lips have different colors (as in *Collinsia* and *Viola pedata bicolor*), but more commonly the variegation is due to spots or lines on a background of another color. In some plants with vernal flowers (as *Hepatica*) a group of individuals may exhibit a number of colors, varying from white through pink to blue, thus greatly increasing the showiness of the plant group as a whole. Often flowers that are inconspicuous individually are so massed into compact inflorescences as to produce a showy effect; such a condition is seen in the umbellifers and even more in the composites, where the inconspicuous central or *disk* flowers often are surrounded by showy outer or *ray* flowers, giving the effect of a large simple flower (fig. 479). The inflorescences of *Hydrangea* consist similarly of inconspicuous central and of showy outer flowers, the latter being sterile. In some plants the calyx is the showy organ (as in *Abronia* and *Mirabilis*), and in some species of *Castilleja*, *Euphorbia*, and *Monarda* the bracts, or even the upper leaves, are much showier than are the relatively insignificant flowers. In some dogwoods the involucre is much showier than are the flowers, and in the willows where there is no perianth, the staminate catkins often are showy by reason of the conspicuous stamens.

Zygomorphy. — *Zygomorphy* or irregularity in the corolla often adds to the conspicuousness of flowers. Many flowers are *labiate* or lipped (as in the mints and the legumes), the lower *lip* commonly protruding farther than the upper (fig. 480); the culmination of lip development and zygomorphy is found in the orchids, whose flowers are noted for their bizarre shapes. The projecting lower lip is of obvious advantage as a landing place for pollinating insects, notably the bees. Often, as in the flowers of many legumes, the weight of the insect presses down the lip sufficiently to expose the anthers and the stigma. Floral lips are of no advantage for the hawk moths and for similar insects, which hover before the flowers without alighting. As

a class, actinomorphic flowers are erect, contrasting with the generally lateral display of zygomorphic flowers (fig. 480), which thus are well suited for insects that alight on lips or hover before the flowers.

Odor. — The attractiveness of flowers to insects is in large part due to their fragrance. Most fragrant flowers are also showy (as in the lilacs, roses, crabs, and water-lilies), but some very fragrant flowers are inconspicuous (as in the grape and mignonette), just as some very showy flowers are without appreciable odor (as in the poppy). In many plants (as in *Smilax herbacea* and *Trillium erectum*) the odor, though offensive to human nostrils, attracts certain insects. Some flowers that are relatively odorless by day are very fragrant at night (as in species of *Silene*). Flower fragrance commonly is due to the escape of volatile oils into the atmosphere. A remarkable case of floral dimorphism is seen in *Renanthera*, a tropical orchid; most of the flowers are white and inodorous, but at the base of the inflorescence are two fragrant yellow flowers which bloom first and remain fresh and fragrant until all the other flowers have gone.

The sensitiveness of pollinating insects to color and to odor. — It is believed commonly that odors and bright colors in flowers are of great importance as indicators (or " signals ") to insects of the presence of nectar or pollen, and some observers even go so far as to suppose that these features have arisen through natural selection, the insects preferring the more fragrant and showy flowers, while others go unpollinated, so that the plants bearing them have no progeny. There is no evidence whatever for the selection theory of the prevalence of showiness and odor, and even the theory that insects are attracted by color and by fragrance rests too little on experiment and too much on the untenable assumption that the theory must be true, because nobody knows any other rôle for these floral features. It is a tenable hypothesis that such features are without value to the flowers possessing them, and the " signal " theory deserves support only as it is proven experimentally.

It is not certain that insect attraction is the only possible rôle of colored corollas; it has been suggested that they may play an important part in the chemistry of fruit maturation. Pigmented plastids may be important in food making, and pigmented cell sap may indicate the formation of useless by-products. It is to be noted that some wind-pollinated flowers are very showy, as in the larch and the red maple. Corollas also are of some importance as protective organs for the pollen and stigmas, especially in flowers whose corollas close at night and in stormy weather.

The possession of a keen sense of odor by pollinating insects is undoubted, inconspicuous fragrant flowers being visited much more than are showy odorless flowers. The readiness with which flies are drawn to sources of nauseous odors is well known, and they frequent ill-smelling flowers in a similar fashion. Hawk moths have been found to be able to detect at a distance of several meters the presence of fragrant but invisible nocturnal flowers, and bees have been seen to fly directly toward honey artificially hidden. Indeed, there are reasons for believing that many insects are able to detect odors that are inappreciable to human nostrils.

The possession of a keen sense of color is much less certain. Even the ardent supporters of the " signal " theory hardly postulate it except for the more specialized insects, such as butterflies and bees. The best experiments indicate that insects are very short-sighted, none being able to see distinctly for more than sixty centimeters and bees very much less than that. Objects in strong contrast (such as large light and dark bodies in juxtaposition, or bodies in motion) appear to be seen much farther than are other objects, certain Lepidoptera seeming to be able to see thus vaguely for a meter and a half, and bees for a half meter. The only insects in which color perception has been definitely demonstrated are the honeybees (*Apis*). These highly organized insects often have been seen to visit gaudy but nectarless artificial flowers, and sometimes they attempt to get at showy natural flowers that are under glass. Frequently they visit colored, unopened buds and wilted flowers, the latter being at times approached, even after they have fallen to the ground. Apiarists rather generally believe that honeybees are able to perceive color differences, and hence they sometimes paint their hives in different colors, so as to aid the bees in recognizing their abode. To the extent that color is perceived by insects, it is a much more reliable " signal " than odor, since the latter often is affected by the wind or masked by other odors. Probably the characteristic forms of flowers serve as indices to nectar, especially in the case of flowers that are conspicuous by their shape or by their size; some observers think that form is even more important than color as an insect " signal."

Some investigators believe that honeybees not only perceive colors, but that they have marked color preferences. Experiments with honey on colored papers seem to show that bees tend to visit a particular color, even if others are more conveniently situated, and elaborate theories have been worked out on the assumption that bees dislike yellow and prefer blue, whence it seems to some observers an easy postulate

that the day of yellow flowers is waning and that of blue flowers is in the ascendant. Such conclusions certainly are unwarranted. The constancy of the honeybee to a given color, such as blue, does not mean a preference for blue as such, but the association of nectar or pollen with that color. If a bee commences its activities on a red flower, or on honey placed on a red paper, it is constant to red. In visiting flowers, bees are constant not only to color, but also to form, flying from flower to flower of the same species. This constancy to a given plant species for a certain period is of great advantage to the plant, since it means a minimum waste of pollen. It is equally of advantage to the bees, since the nectar or pollen is all of the same quality, and since time and energy are saved in that exactly the same process is

FIG. 481. — A colony of morning glories (*Calystegia soldanella*) in dune sand; note the striking contrast in tone between the flowers and the foliage, illustrating the possibility of floral showiness even for color-blind insects; New Zealand. — From COCKAYNE.

repeated in each flower that is visited. The collapse of the color preference theory is well shown in those cases in which different individuals of a given plant species have flowers of different colors. In such species bees soon learn the essential likeness of the differently colored flowers, going from one color to another indifferently. In other words, bees learn to ignore differences in color that are unaccompanied by differences in nectar or pollen. Even if bees prove to be the only insects with a color sense, other insects certainly are able to appreciate differences in tone, as they appear in a photographic print (fig. 481), where whites and various colors come into sharp contrast with the darkness of the foliage. Similarly, the prevalent whiteness of nocturnal flowers makes them more conspicuous than would any pigment color.

Memory and instinct. — When bees are taken to a new feeding ground, their first flights are more or less misdirected and haphazard, resem-

bling the habitual movements of such insects as the flies. Soon they appear to be attracted by various odors or colors, and after some days they show their accustomed rapid and precise movements. That is, memory appears to replace both odor and color as the directive stimulus of first importance. Probably many discordant results of various observers can be harmonized if the memory factor is taken into account. There are some cases where instinct seems to be the controlling factor, as in the pollinating insects of the figs and the yuccas (pp. 375–379).

Many experiments with bees show the importance of the memory factor. When showy flowers are deprived of their corollas, the number of visiting bees at first is small, but after a time the insects become accustomed to the new conditions and visits become numerous. In some such experiments the seed production is less than in flowers with corollas, but this may be due to lessened protection of the ovary or to a less effective dusting of the stigmas with pollen. If flowers are artificially hidden by leaves, bees soon learn the new conditions, and the visits which at first are few soon become frequent. Similarly bees soon learn to visit wind-pollinated flowers if there is placed on them honey and water, or sugar and a fragrant volatile oil. The ability of bumblebees to learn is shown by *Bombus terrestris*, which has a proboscis too short to get honey from *Aquilegia vulgaris;* after vain attempts to reach the nectar in the ordinary way, it has been seen to bite a hole in the spur and suck it out, repeating the process thenceforth. Similar holes are bitten in the spurs of *Tropaeolum* by *Bombus hortorum*.

Concluding remarks. — As a directive stimulus, insuring the visitation of flowers by insects, odor seems to be more important than color, because it is distinguished from a much greater distance and by a much larger number of insects; in the higher insects, notably among the bees, which do most of the pollinating, memory seems to be a still more important factor. In the majority of flies and in most lower insects it is doubtful if either color or memory plays a very conspicuous part, the odor sense here being regarded as the most important. Odor is of particular significance where flowers grow in masses. So far as color and form play a part, it is only in the immediate vicinity of the flower and in the most general way. The elaborate theories which assign a distinct rôle for each floral form and for each shade of color, which regard the lines and spots on the corolla as guides to the nectar,[1] and which relate the showiness of alpine flowers to the paucity of insects have no support from exact observation and experiment.

Features favoring the sprinkling of insects with pollen. — In most flowers, especially in those that are open and actinomorphic, the anthers

[1] Striking spots or lines may occur in such nectarless flowers as that of the poppy.

are exposed so conspicuously and the pollen is so abundant that visiting insects scarcely can avoid getting more or less pollen on their bodies, even if they are searching only for nectar; of course, much pollen must adhere to all pollen-gathering insects. In the composites the dense massing of flowers into heads greatly facilitates pollen removal, since the visiting insects necessarily crawl over numerous flowers with their exserted stamens. In many flowers, especially in those which are zygomorphic or which contain but little pollen, there often are specialized features that facilitate pollen removal. Certain parts of the body (chiefly about the head) may receive the pollen somewhat locally; in certain flowers exserted stamens often are grasped by the alighting insect in such a way that the under parts of the body receive the pollen.

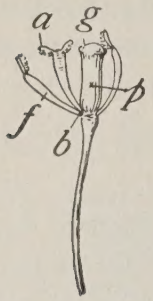


FIG. 482. — A barberry flower (*Berberis thunbergii*) with the calyx and corolla removed, so as to show the pistil (*p*) and the hypogynous stamens, which at maturity lie back upon the inner surface of the petals; when an insect comes in contact with the base (*b*) of the filament (*f*), the latter flies forward, assuming the position of the stamen at the right, and pollen is dusted on the insect and on the stigma (*g*); note that the filaments (*f*) broaden toward the apex, and that the anther valves (*a*) open upwards, being hinged at the filament apex.

Some flowers with *introrse* anthers (*i.e.* opening inwards), as in the gentians, have nectar to the interior of the stamens, while some flowers with *extrorse* anthers (*i.e.* opening outwards), as in *Iris*, have nectar to the exterior of the stamens. Often the stamens grow rapidly just before dehiscence (as in *Parnassia*), assuming a position corresponding to that of the stigma. In a number of instances the insect occasions the release of the pollen, as in the legumes, where the alighting of a bee causes the anthers to protrude suddenly from the enclosing petal and to sprinkle pollen over the visitor. In *Pyrola* and *Kalmia* the anthers are held in unstable equilibrium, and the sudden release coming with the insect visit causes the pollen to be shaken out. In various ericads with pendulous flowers the stamens have appendages, which are likely to be struck by visiting insects in such a way as to result in the scattering of the pollen. Sensitive mechanisms occur also in *Lopezia*, where a petal-like structure holds the single stamen in unstable equilibrium, in *Berberis*, where the stamen itself is sensitive to contact (fig. 482), in *Galeopsis*, where contact causes the anther lids to fly open, and in *Crucianella*, where the style is held in unstable equilibrium until the flower is touched, whereupon the style is suddenly released, bringing out with it a shower of pollen. In *Salvia*, in which there is a swinging anther, an entering bee so presses against the lower arm of the lever as to dust himself with pollen from the upper arm (figs. 472–475). In orchids the pollen masses (*pollinia*) have an exposed adhesive disk, which sticks to the head parts of a visiting insect. The somewhat similar pollinia of milkweeds have clips that fasten about the feet of the insect.

Features favoring the deposition of pollen on stigmas. — Stigmas, as previously noted, secrete sticky substances, and their hairy or papillate surfaces still further favor pollen reception (fig. 464). In many plants the stigmas at maturity have essentially the same position as that of the mature anthers (as in the figwort, figs. 484, 485), so that the part of the insect which is covered by pollen is likely to touch the stigma. In many other cases (as in the violets) the stigma projects beyond the anthers, so that it is likely to receive pollen from the entering proboscis.

In *Centaurea* mechanical irritation (as from a visiting insect) causes the filaments to contract, thus exposing the stigma to pollination by the visitor. The most remarkable situation is in the orchids, where the pollinia above noted, after removal from the flower, move into such a position that they are likely to come into contact with the stigma of the next flower visited. The orchid stigmas remain receptive a remarkably long time if potent pollen fails to come in contact with them, though they wither soon after the proper pollen begins to germinate. The corollas also remain fresh on unpollinated flowers some days or even weeks longer than on pollinated flowers.

Features which impede close-pollination and facilitate cross-pollination. — *Mechanical features impeding close-pollination.* — In a vast number of flowers close-pollination is difficult or even impossible. Frequently the stigma projects beyond the anthers (as in certain lilies and evening primroses), so that pollen cannot fall upon the stigma of the same flower (fig. 480); in pendulous flowers, of course, the stamens would have to project beyond the stigma to have a like result. Sometimes, as in *Iris*, the receptive surface of the stigma is so oriented that the insect rubs against it upon entering, but not upon leaving the flower, thus facilitating cross-pollination and preventing close-pollination. Close-pollination is difficult in flowers with extrorse anthers. In orchids it is almost impossible for the pollinia to come into contact with the stigma of the same flower; in some lady's slippers (as in *Cypripedium calceolus*) the insect enters and leaves the flowers by different routes, brushing the stigma upon entering and the anthers before leaving.

Dichogamy. — The commonest floral feature that facilitates cross-pollination and makes close-pollination difficult is *dichogamy*, or the consecutive maturity of anthers and stigmas, contrasting with simultaneous maturity or *homogamy*. Dichogamy may be complete, that is, the pollen may be shed before the stigma matures, or the stigma may

wither before the pollen sheds; more commonly it is incomplete, that is, there is a partial overlapping of the periods of stigmatic receptiveness and of the shedding of pollen. Stigmas commonly remain receptive (especially when unpollinated) for a longer time than that required for the shedding of the pollen, hence cross-pollination is more likely to result when flowers are *protandrous* (*i.e.* with the anthers maturing first) than when they are *protogynous* (*i.e.* with the stigmas maturing first); however, pollination of some kind, either cross or close, is more likely to result when the flowers are protogynous, because of the greater likelihood of overlap in the latter case.

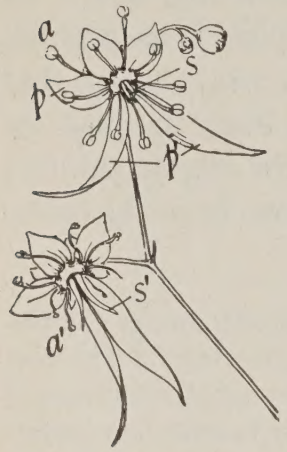
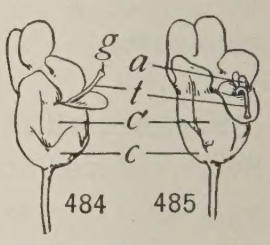


FIG. 483. — Flowers of a saxifrage (*Saxifraga sarmentosa*), illustrating protandry; in the younger (upper) flower, the anthers (*a*) are mature and the pistils (*s*) immature; in the older (lower) flower, the anthers (*a'*) have shed their pollen and the pistils (*s'*) have become mature; note that the corolla is zygomorphic, three of the petals (*p*) being short and two long (*p'*).

Probably the number of protandrous and protogynous species is about equal, though there are a greater number of conspicuously protandrous forms, such as the saxifrage (fig. 483), the evening primrose (in which the anthers may shed before the corolla opens), the composites, and the umbellifers, than there are of conspicuously protogynous forms, such as the figwort (figs. 484, 485) and the crucifers. A striking case of protogyny occurs in *Aristolochia clematitis*, where the interior of the narrow calyx tube is lined with reflexed hairs. Insects enter easily and crawl over the mature stigma, but on account of the stiff hairs they cannot leave until the anthers mature, when they become dusted with pollen; the subsequent withering of the calyx hairs permits their exit, and upon their entering another flower, cross-pollination takes place.

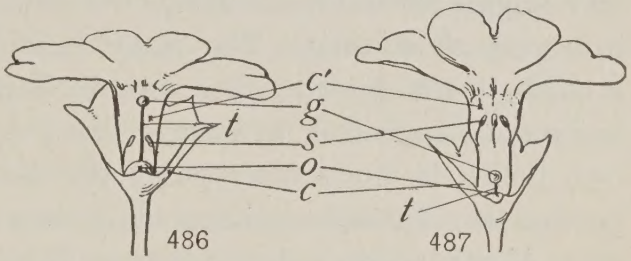


FIGS. 484, 485. — Flowers of the figwort (*Scrophularia marilandica*), illustrating protogyny: 484, a young flower with a prominently exserted style (*t*) and a receptive stigmatic surface (*g*); 485, the same flower a day or two later, with its style (*t*) declined and out of the way of visiting insects, the stamens having grown sufficiently to expose the anthers (*a*) to such pollinating agents; note that the sympetalous corolla (*c'*) is bilabiate; *c*, calyx.

In most dichogamous flowers the stigmas and the anthers, though usually occupying the same position consecutively, nevertheless are out of the way of the one, when the other is mature. In the mallows the anthers at first hide the stigmas, but later bend back and expose them, while in *Salvia*, the style which at first is short grows out after the pollen is shed, assuming a favorable position for pollen reception by the stigma. In the figwort, which has a protogynous flower, the style bends back over the lip after maturity (fig. 485). In *Parnassia* one stamen after another assumes a position where visiting insects are likely to

come into contact with them. In most dichogamous flowers (but not in *Aristolochia*) two insect visits are necessary if both pollen and stigma are to play a part in pollination; this is an apparent disadvantage as compared with homogamous flowers.

Heterostyly. — A highly specialized condition that opposes close-pollination and favors cross-pollination is that known as *heterostyly*, in which the stigmas and the anthers in different flowers occupy different positions. Most such flowers are actinomorphic, and they are illustrated by the primrose, flax, forget-me-not, and bluets. In the primrose some plants have flowers with long styles, the stamens being attached toward the base of the corolla tube, while other plants have flowers with short styles and with the stamens attached toward the upper part of the corolla tube (figs. 486, 487). In *Lythrum salicaria* there are three kinds of flowers, one with long styles and intermediate and short stamens, another with short styles and intermediate and long stamens, and a third with intermediate styles and long and short stamens. The same part of the insect that comes in contact with the lower stamens will touch the stigma of a short-styled flower, while pollen from the upper stamens will come in contact with the stigma of a long-styled flower, thus insuring cross-pollination.



FIGS. 486, 487. — Longitudinal sections through flowers of the Chinese primrose (*Primula sinensis*), illustrating heterostyly: 486, a flower with a long style (*t*) and with stamens (*s*) inserted near the base of the corolla tube (*c'*); 487, a flower with a short style (*t*) and with stamens (*s*) inserted at the median part of the corolla tube (*c'*); that part of a visiting insect which strikes the anthers of one flower will be likely to strike the stigma of the other, thus effecting cross pollination; note that the corolla tube of 487 is dilated where the stamens are inserted; these flowers illustrate perigyny; *c*, calyx; *o*, ovary.

Commonly the upper stamens of heterostyled flowers have large pollen grains corresponding to the large long-haired stigmas of the long-styled flowers, while the lower stamens have small grains corresponding to the small smooth stigmas of the short-styled flowers; the corollas and other organs also may differ considerably. Some investigators regard the large size of the pollen grains of the upper stamens as advantageous, since their pollen tubes have to traverse a greater distance upon germination; this view, which is doubtful *a priori* on account of their parasitic nourishment, has been experimentally disproven.

Impotent and prepotent pollen. — So far as the prevention of close-pollination is concerned, the most specialized flowers are those in which

the pollen of a given flower is *impotent* (*i.e.* unable to initiate seed production) on the stigma of the same flower. Complete impotence is comparatively rare, well-known cases being found in *Corydalis cava*, *Hemerocallis fulva* (day lily), *Fagopyrum esculentum* (buckwheat), *Secale cereale* (rye),[1] and also in several of the Leguminosae, but there are many plants in which *foreign* pollen (*i.e.* pollen from other flowers) is *prepotent* (*i.e.* more or earlier effective) on a given stigma than *own* pollen[2] (*i.e.* pollen from the same flower); foreign pollen that is sown on a stigma several hours after own pollen often gains the ascendency in a very short time. The acme of impotence is found in various orchids, in which own pollen actually is prejudicial to the stigmas (or *vice versa*), appearing to behave like a poison. In the Leguminosae own pollen is much more potent in the annual species than in the perennials. In some legumes (as *Cytisus laburnum*) the usual impotence of own pollen is due to the fact that the pollen tube cannot penetrate the cuticle of the stigma; when this is ruptured artificially, own pollen is potent. In *Corydalis cava* own pollen frequently germinates, but the pollen tube is unable to penetrate to the ovules.

In nearly every case pollen from a given flower is no more potent on other flowers of the same plant than on the stigma of the flower that produced it, thus showing in a most striking way that geitonogamy is essentially the same as autogamy and should not be classed with xenogamy. In a number of cases own pollen appears sometimes to be impotent, and sometimes variously potent (as in *Eschscholtzia* and in *Brassica rapa*), possibly by reason of varying external conditions. From the viewpoint of pollen potency, therefore, there are three classes of plants: (1) those in which own pollen is as potent as foreign pollen, forming a class with numerous representatives (as *Oenothera* and most crucifers); (2) those in which foreign pollen is prepotent, also forming a class of large size; and (3) those in which own pollen is impotent, forming a comparatively small class.

Among the most remarkable examples of impotence are those afforded by heterostyled flowers, own pollen being completely impotent in *Linum*, and slightly potent in *Primula*.[3] The most extraordinary

[1] Even in rye geitonogamy may occur.

[2] However, the pollen must not be too foreign, as from another genus or family. Thus impotence is found at the extremes of relationship, that is, where pollination occurs between anthers and stigma in the same flower or in flowers of distantly related plants.

[3] Some observers report the complete potency of own pollen in some species of *Primula*.

feature of these plants, however, is that cross-pollination between the anthers and stigmas of different position in separate plants is quite as ineffective as is close-pollination, thus showing clearly that the cause of impotence is not wholly closeness of relationship, but something as yet unknown. A possible advantage of this peculiar phenomenon is seen in the fact that the progeny of individuals which are close-pollinated, or of individuals where there is cross-pollination between anthers and stigmas of different position, usually is made up of plants with but one kind of flower. If cross-pollination is advantageous (see p. 381), the combination of heterostyly and impotence in own pollen would seem to be particularly advantageous, since own pollen is scarcely likely to be deposited on a stigma, and if it should chance to lodge there, it would not initiate seed production.

Dicliny. — Dicliny, which commonly is regarded as a primitive floral feature, is more characteristic of wind-pollinated than of insect-pollinated plants, but it is far more common in the latter than formerly was supposed, and there is almost certain proof of a strong evolutionary tendency from monocliny to dicliny, as in the figs and in many composites. Among the diclinous insect-pollinated species that probably are primitive, the best known are the willows, which are dioecious. Some investigators doubt whether as many as half of the plants that appear to be monoclinous are so in fact. A large number of species have both monoclinous and diclinous flowers on the same or on different plants; the maples illustrate this condition, some of them (as the box elder) appearing to have become completely dioecious. Certain cultivated varieties of the strawberry exhibit similar features.

Asparagus appears to have become essentially dioecious, since the stamens of some plants and the pistils of others appear to play no part in pollination. Many species (as in the grape and the horse chestnut) have been found to possess impotent pollen in some flowers, and non-receptive stigmas in others. *Rhamnus lanceolata*, a heterostyled species, seems to be approaching dioecism, since the short-styled flowers produce the most seed, while the long-styled flowers have but little pollen and that small-grained. Many plants have organs occupying the position of stamens, which now play no direct part in pollination, whatever may have been the case formerly; notable illustrations are the so-called sterile stamens of *Parnassia* (now nectar-secreting organs) and of *Pentstemon*.

Much the most significant tendency toward dicliny is seen in the composites, which commonly are regarded as the highest family of plants. In this family there are three common floral conditions, that in which all the flowers are actinomorphic and inconspicuous (as in *Eupatorium*), that in which all the flowers have conspicuous strap-shaped (ligulate), zygomorphic corollas (as in the dandelion, fig. 488), and

that in which there are actinomorphic and inconspicuous disk flowers, surrounded by petal-like zygomorphic ray flowers; the third group is much the largest and includes the asters, goldenrods, and sunflowers (fig. 479). Perfect monocliny is confined essentially to the second and to a part of the first group, so that a greater or less amount of dicliny characterizes the majority of this great family. In the third or ray-flowered group there are three common conditions: (1) that in which all flowers are seed-producing, the disk flowers being monoclinous and the ray flowers pistillate (as in *Aster*); (2) that in which the disk flowers are monoclinous and the ray flowers reduced essentially to corollas (as in *Helianthus*); and (3) that in which the disk flowers are monoclinous but with the pistils sterile, while the ray flowers are pistillate (as in *Polymnia*); *Silphium* belongs in the last group, but it seems to have progressed still more toward dicliny, since the styles of the disk flowers do not even fork into stigmas.

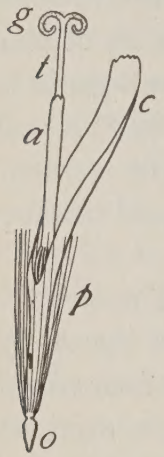


FIG. 488. — A flower from a dandelion head (*Taraxacum officinale*), illustrating epigyny; note the achene (*o*), the capillary pappus (*p*) representing the calyx, the strap-shaped, five-toothed, sympetalous corolla (*c*), the tubular column of syngenesious anthers (*a*) surrounding the basal portion of the style (*t*) and the two recurved stigmas (*g*).

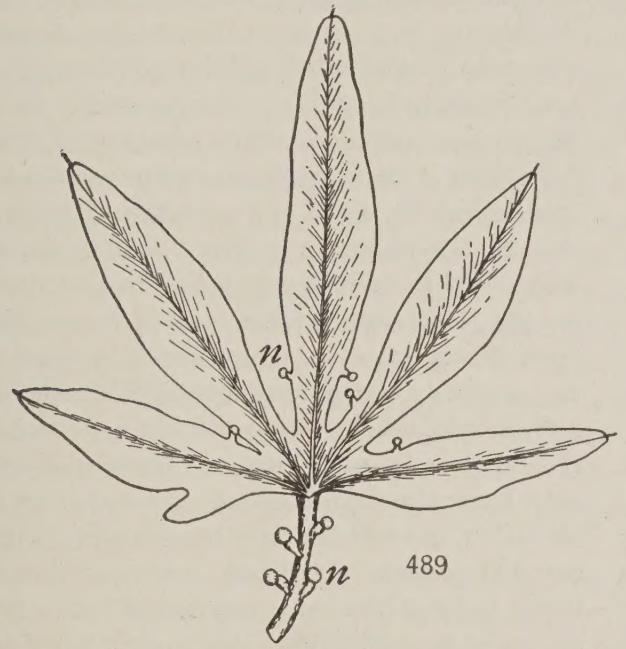
Composites without ray flowers show as much diversity as do the ray-flowered forms, though the latter are much more numerous. Some forms have all flowers alike and monoclinous (as in *Eupatorium*). In *Artemisia* the heads in some species consist of monoclinous and pistillate flowers, while in other species they consist of monoclinous but sterile disk flowers and of pistillate marginal flowers. *Iva* exhibits monoecious dicliny, the inner flowers being staminate and the outer pistillate. *Ambrosia* and *Xanthium* also are monoecious, but the two kinds of flowers are in separate heads. The evolution of dioecism from monoecism appears to be illustrated by *Petasites*, for though all heads have monoclinous but sterile central flowers and pistillate marginal flowers, some plants have heads with many staminate and few pistillate flowers, while other plants exhibit the reverse condition. *Gnaphalium alpinum* is essentially dioecious, since in some plants the stamens do not shed pollen, while in others the pistils are sterile. Complete dioecism is illustrated by the related *Antennaria*. Some composites, notably *Ambrosia*, are wind-pollinated, as well as diclinous. The possible significance of the remarkable floral diversity of the Compositae will be considered elsewhere (p. 392).

The protection of flowers from deleterious insects. — *Deleterious kinds of insects.* — Crawling insects, such as the ants, are disadvantageous floral visitors, since the pollen they carry is likely to be brushed off as they crawl from flower to flower. Even among the flying insects, where such pollen losses are reduced to a minimum, those that fly about in a haphazard manner, visiting various plant species in succession, are far less beneficial than are such insects as the bees, which on any given day visit individuals of the same plant species with consistency. It has often been supposed that various floral features are highly advantageous because they exclude certain insects, but the evidence for this view in many cases is more imaginary than real. In any case, it is not to be supposed that the development of such features

has had any relation to deleterious insects; so far as they have value in this connection, it must be regarded as purely incidental.

Hairs and glandular surfaces. — Stiff bristly hairs have been thought to serve as barriers against various crawling animals, especially snails. Glandular hairs doubtless are still more effective, and it is noteworthy that they abound on floral stems more than elsewhere. Perhaps the most undoubted instance of such protection is *Silene*, some species of which (as *S. antirrhina*) develop just at anthesis an extensive glandular surface on the upper stem internodes; insects are caught by these plants so frequently as to have led to the common name of catchflies.

Extrafloral nectaries. — On many plants there occur *extrafloral nectaries* (*i.e.* nectar-secreting organs apart from inflorescences), as in various legumes, and in



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FIGS. 489, 490. — Extrafloral nectaries on the leaf of a passion flower (*Passiflora*); 489, a palmately five-lobed leaf with nectaries (*n*) on the petiole and also on the blade; 490, a single nectary (*n*) with a large drop of nectar (*d*); considerably magnified.

Ricinus and *Passiflora* (figs. 489, 490). Usually they are most abundant on the upper side of the petioles and on the under side of the leaf blades. Ants frequently visit these nectaries for food, and it commonly has been supposed that the organs thus are advantageous to plants, the view being that the insects are satisfied with what they obtain from the extrafloral nectaries and thus keep away from the flowers, where the rifling of the floral nectaries might endanger cross-pollination. It has even been held that nectar-feeding ants are combative and keep off leaf-cutting ants and other harmful insects. There is no valid evidence for these fanciful theories, and careful experiments in which plants have been deprived of extra-floral nectaries without affecting seed production or other plant activities would seem to make them untenable. Indeed, the greater frequency of the visits of ants to the nectary-bearing individuals has been shown to lead to more flower-rifling than in the plants deprived of nectaries. In some cases, as in *Vicia*, bees have been observed to visit extrafloral nectaries in preference to floral nectaries; in such

a case also extrafloral nectaries are a positive disadvantage to plants. Furthermore, in many plants the chief secretion of nectar occurs before and in others after anthesis; rarely, if ever, is there any exact correlation with this period, as in the case of floral nectaries. The theory that these nectaries have no rôle of importance is more tenable than the theory of protection from ants. This view of the case is supported by the fact that extrafloral nectaries occur in flowerless plants, as in *Pteris* and in various other ferns.

Flower structure. — Many flowers are so constructed that certain flying insects, as well as ants, are unable to disturb the pollen or nectar; this is most obvious in flowers with long corolla tubes and in zygomorphic flowers. In flowers with long corolla tubes (such as the petunia, fig. 491), or with long spurs, only such insects as various Lepidoptera, which have corresponding elongated mouth parts, can reach the nectar; in some cases the corolla tubes are lined with bristly hairs which still further tend to keep out small insects, though they offer practically no obstruction to long probosces. In a number of zygomorphic flowers (as in the snapdragon and in various legumes) it is difficult for small and weak insects to force their way to the nectar or pollen. Among the features which tend to exclude undesirable insects, floral zygomorphy, long corolla tubes, and spurs are much the most important. Since insects with long mouth parts can get freely exposed nectar, the chief value of zygomorphy and tubular corollas would seem to be the exclusion of undesirable insects. While such structures may have some evolutionary connection with insect visitation, the connection is too complex to be understood at present. It would seem much better for a flower to be pollinated in any manner than to run the chance of no pollination if the proper insect were not present. The significance of flower structure, here as elsewhere, is an unsolved enigma.

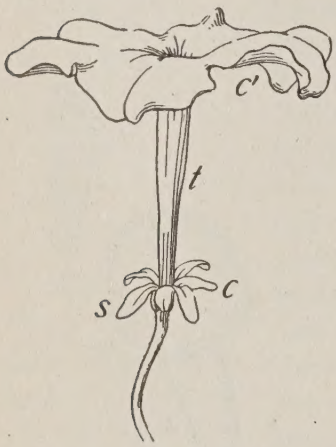


FIG. 491. — A flower of *Petunia;* note the long tube (*t*) of the sympetalous corolla (*c'*), well-fitted for pollination by moths with long mouth parts; *c*, calyx of five sepals.

Some instances of specialized cross-pollination. — *General remarks.* — The consideration of cross-pollination cannot be concluded without a short account of some of the more striking instances of extreme specialization. In some of the cases to be mentioned the dependence of the flower upon the insect (and often of the insect upon the flower) is absolute, and therefore to be regarded as illustrating obligate symbiosis. When such specialized forms are taken to other countries for cultivation, they may not produce seed, unless the insects also are transported.[1]

Silene and the orchids. — Some of the night-blooming catchflies (*Silene*) are visited by nocturnal Lepidoptera, especially *Dianthoecia*, whose movements in getting nectar incidentally effect pollination; later the moth deposits eggs in the ovary with its long ovipositor, and the developing larvae feed upon the ovules. In

[1] An excellent illustration of this is afforded by the orchid, *Vanilla*, whose fruits furnish commercial vanilla; the absence of the proper pollinating insect in certain regions makes artificial pollination a necessity for profitable cultivation. The day lily (*Hemerocallis fulva*) never fruits in Europe, probably because of the absence of the proper insect.

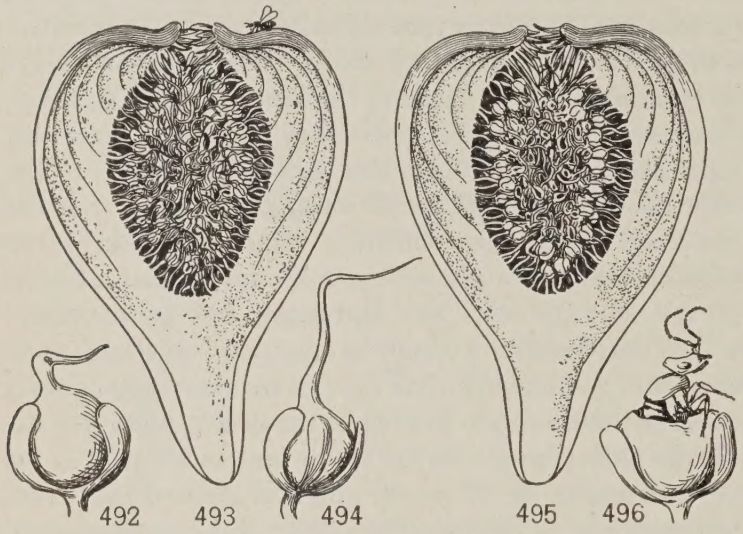
such an instance symbiosis is more obligate for the insect than for the flower. The orchids, as a class, show the most extreme floral specialization, dependence upon some particular insect often being obligate.

Arum. — In *Arum*, although entirely different structures are involved, there is much to recall the cross-pollination of *Aristolochia* (p. 368). The inflorescences are composed of staminate flowers above and of pistillate flowers below, which are arranged on a club-shaped central axis, the *spadix*, and enclosed within a large bract, the *spathe*, which, though enlarged below, is considerably constricted above. At anthesis the flowers give forth a nauseous odor that attracts numerous small flies, whose exit for a time is said to be barred by reflexed hairs between the pistillate and staminate flowers and in the narrow passageway above. The pistillate flowers mature first, and when the staminate flowers mature, the lower ring of hairs dies, permitting the insects to crawl over the stamens, where they become covered with pollen. Very soon the upper ring of hairs withers also, permitting escape to the exterior. If the insects visit another inflorescence at once, it is evident that the mature pistillate flowers are likely to be cross-pollinated. Since *Arum*, as well as most other aroids with similar features, is monoecious, it is obvious that a highly specialized mechanism of this sort prevents not autogamy, but geitonogamy. Later observations call most of this familiar account in question, especially as to *Arum maculatum*. In this species it is claimed that the exit for the visiting flies is not barred, since the hairs are not stiff enough to impede the insects and often are not even long enough to fill the passageway. So far as the insects are held in the spathe, it is said to be due to drugging by the plant, and it is claimed that there is a sufficient amount of overlapping in the periods of maturity of the staminate and pistillate flowers to result in geitonogamy. Furthermore, there is no adequate proof that the flies which manage to escape visit other inflorescences sufficiently soon to effect cross-pollination.

The fig. — The most remarkable of the known cases of cross-pollination whose evolutionary development cannot even be imagined, is that of the figs, a group of plants which, like the aroids, are diclinous and commonly placed low in the scale of seed plants. The inflorescence, known as a *synconium*, is unique; the numerous flowers line the walls of a chamber (representing the receptacle) and are entirely hidden (figs. 493, 495). Entrance to the flowers is possible only through a small apical orifice (as in the India-rubber tree, *Ficus elastica*), which is lined with scales. All species of figs are diclinous, some having the two kinds of flowers somewhat indiscriminately mixed; in most species, however, the staminate flowers are toward the top and the pistillate flowers toward the base of the synconium. Some species approach dioecism, certain trees having pistillate and others monoecious synconia. The fig of commerce (*Ficus carica*) is essentially dioecious, the pistillate flowers, of apparently monoecious synconia, being sterile; in rare cases, however, the staminate trees bear some pistillate flowers and even ripen seeds.

The commercial fig is pollinated by a small wasp, *Blastophaga grossorum*, whose life cycle is most extraordinary. The females force their way through the synconial orifice, and this is so difficult of accomplishment that usually they lose their wings in the process; after laying their eggs within the young ovules, they die within the growing fig. Those females that chance to enter the pistillate synconia (which become the figs of commerce) have no progeny, since the flowers have styles of such

length that the insects are unable to lay their eggs in the right spot (fig. 494). But in the staminate figs, known as *caprifigs*, there are short-styled rudiments of pistillate flowers (often called gall flowers, fig. 492), in which eggs may be placed properly, later hatching into wasps. Some stimulus exerted by the insect causes the ovary primordia to develop into seedless galls. After a time the males hatch, eating their way out of the galls in which they developed and into the galls occupied by developing females; copulation is followed by the death of the males within the caprifig. The females thereupon escape (fig. 496), crawling over the staminate flowers of the caprifig and becoming dusted with pollen; those that chance to visit figs incidentally pollinate the stigmas therein, but have no progeny, while those that go to caprifigs have progeny, but are of no service in pollination.



FIGS. 492–496. — Pollination of the fig (*Ficus carica*): 495, a synconium cut longitudinally, showing gall flowers produced by the fig wasp (*Blastophaga grossorum*); near the mouth of the cavity is a female fig wasp, which has escaped from one of the galls; 493, a similar synconium with seed-producing pistillate flowers; near the mouth of the cavity are two female fig wasps, one of which has already crept inside; 492, a short-styled gall flower; 494, a long-styled seed-producing flower; 496, a fig wasp escaping from a gall flower. —From KERNER.

One of the strangest features of a process strange throughout is that the pistillate flowers mature two months before the staminate flowers; however, by the time the latter are mature, another crop of synconia has developed with stigmas ready for pollination, so that stigmas of a given generation are pollinated from inflorescences of the preceding generation. In southern Italy there are three such crops of figs and caprifigs each year (*viz.*, in April, June, and August), and three corresponding generations of wasps. This symbiosis between *Ficus* and *Blastophaga* has been denominated mutualism, but surely it is a somewhat destructive form of mutualism, where death without progeny comes to such a large proportion of the symbionts on each side, namely, to the female insects that enter the figs and to the pistillate flowers of the caprifigs.

Centuries before the process of pollination was discovered, the ancients cultivated the commercially valueless caprifigs, and placed branches with maturing synconia on fertile fig trees; this process, known as *caprification*, makes it easy for the female wasps (which fly weakly, though possessing wings) upon emergence from the caprifigs to enter and pollinate the figs. Caprification and pollination are quite unnecessary for reproduction commercially, since figs always are propagated from cuttings. Caprification is not always necessary, even for the production of commercial figs,

there being some varieties which mature edible fruits (though without viable seeds) without caprification or pollination. Other varieties, notably the Smyrna fig, require pollination for their best development, the caprified fruits surpassing those that are not caprified in plumpness, juiciness, and flavor.

Geitonogamy. — *General remarks.* — In spite of the numerous and remarkable features which facilitate cross-pollination, *geitonogamy* (or pollination between different flowers of the same plant) and close-pollination are very common and, taken together, perhaps are more common in monoclinous flowers than is cross-pollination. Furthermore, there are cases in which the features facilitating these kinds of pollination are about as specialized as any that have been previously noted in connection with cross-pollination. In most species a number of flowers bloom at once on the same plant, so that dichogamy does not prevent geitonogamy, especially because insects usually visit all the flowers on a given plant before flying to another. The first flower on each plant visited may get only foreign pollen, but the chance of geitonogamy increases with the number of flowers visited, though it should be remembered that the general prepotency of foreign pollen greatly favors the latter in initiating seed production. Geitonogamy is commonest in plants with compact inflorescences, especially where these are umbels, spikes, or heads, as in the umbellifers (the highest of the polypetalous dicotyls) and in the composites (the highest of plants). While such floral massing does not exclude cross-pollination, it so greatly facilitates geitonogamy that the latter probably is the chief method of pollination. Although the almost habitual dichogamy of these plants prevents autogamy and peculiarly facilitates geitonogamy there is no adequate evidence that the latter is perceptibly more advantageous than the former.

Illustrations of geitonogamy in the composites and umbellifers. — The culmination of conditions favorable to geitonogamy occurs in the composites, a group that is notably protandrous. The outer flowers bloom first, but the stigmas remain receptive until the flowers next within shed pollen. After the stamens mature, the style elongates, pushing up through the surrounding tube of united anthers and swabbing out some of the pollen, which adheres to the style bristles. Later the style forks, exposing the receptive stigmatic surfaces (fig. 488), which with the adherent pollen commonly come into contact with the stigmatic surfaces of adjoining flowers. Entangled style branches of this sort are especially conspicuous in *Eupatorium.* In contrast to pollination by wind or insects, this may be termed *contact pollination.* Geitonogamy by contact is especially characteristic of the milky-juiced composites (such as the dandelion, figs. 499, 500), since the heads open by day and close at

night and in rainy weather, insuring to an unusual degree the contact of stigmas and pollen-covered organs of adjoining flowers.

In composites with conical or columnar receptacles (such as *Rudbeckia* and *Lepachys*), there occurs what may be termed *gravity pollination*, pollen from the upper flowers dropping upon the stigmas of the lower and older flowers. In *Anthemis*, as the flowers develop, the disk elongates in such a way that the stigmas of the older flowers are exactly under the shedding stamens of the younger flowers. It will be recalled that in those composites that tend toward dicliny, it is the outer (older) flowers that ordinarily are pistillate, and the inner (younger) flowers that ordinarily are staminate. So far as geitonogamy is concerned, such a condition is economical, since stamens would be useless in the outer flowers and pistils in the inner flowers, though they might be of value in case of cross-pollination by insects.

The structural facilitation of geitonogamy in the umbellifers is almost as marked as in the composites. In *Eryngium* the flowers are in dense heads that facilitate contact pollination between adjoining flowers. In *Sanicula* there are monoclinous and staminate flowers, the long styles of the former bending over and bringing the stigmatic surfaces into contact with the latter. In such wind-pollinated composites as *Ambrosia*, geitonogamy is likely to take place between flowers of different heads, as the staminate heads are uppermost.

Close-pollination or autogamy. — *General remarks.* — *Autogamy*, that is, pollination between anthers and stigmas of the same flower, once thought to be relatively rare, is now known to be extremely common. In some cases the features that facilitate autogamy are quite as striking as are those previously mentioned features that impede or prevent it. Autogamy by contact may be called *self-pollination*, a term often incorrectly made synonymous with autogamy in general; as with geitonogamy, close-pollination occurs chiefly by contact or through the agency of gravity, though wind and insects also may be operative. In many cases, especially where foreign pollen is prepotent over own pollen, autogamy probably is effective only in the absence of cross-pollination; in many other cases both appear to be equally effective, and in a number of instances autogamy is the only form of pollination possible. Careful study has shown that in alpine and arctic regions autogamy habitually exceeds xenogamy.

Illustrations of autogamy. — Simple cases of autogamy occur in *Trillium* and in *Geranium*, the anthers and stigmas being in close juxtaposition; most such flowers are slightly protogynous, so that cross-pollination may occur before there is a chance for contact pollination. Somewhat more complex are the many cases in which anthers and stigmas come into contact through growth movements, as in the stamen movements of *Circaea* and of many crucifers, and in the style movements of *Epilobium* and of many other plants; such flowers also are as a rule slightly dichogamous. In the composites autogamy as well as geitonogamy may take place through style

inflections and through the closing and the opening of heads; similarly, many flowers that open and close daily may exhibit autogamy (as in *Gentiana*). Pollen drops directly on the stigma, illustrating gravity pollination in many erect flowers with styles shorter than the stamens (as in the lilac), and in many pendulous flowers with styles longer than the stamens (as in *Dodecatheon*). In *Pedicularis* the growing corolla rubs over the anthers, so that the pollen falls upon the stigma underneath. In *Cyclamen* and *Moneses* the growth curvatures of the flower stalk at the time of anther maturity cause the pollen to drop out upon the stigma.

Yucca. — The flowers of *Yucca* commonly are pendent (fig. 498), and though the stigmas extend beyond the anthers, pollination by gravity is unlikely if not impossible. The flowers are nocturnal, blossoming but once, and are pollinated by a small moth, *Pronuba*. The females pierce the ovaries with their ovipositors and lay eggs among the ovules, before and after which they deliberately take pollen from the anthers, holding it in their specially constructed maxillary palps, and ram it into the stigma. As a result of this astounding process the ovules develop; each larva eats about twenty, and the rest develop into seeds. This symbiosis is believed to be obligate for each symbiont; in any event, *Yucca* is seedless in the absence of *Pronuba*. The mode of evolution of an instinct that impels an insect to stuff a stigma with pollen cannot even be imagined.[1]

Cleistogamy. — The culmination of structures facilitating close-pollination is found in flowers that never open, since in these with rare exceptions autogamy alone is possible. Flowers that regularly open, such as those heretofore considered, are termed *chasmogamous*, while flowers that never open are called *cleistogamous*. Cleistogamy may be habitual (as in the subterranean flowers of *Viola* and *Polygala*), or it may be facultative, depending upon definite external factors. Conspicuous cases of facultative cleistogamy are found in *Oxalis*, *Specularia*, *Impatiens*, and *Lamium*. Subjection to low temperature is believed to be the chief cause of such cleistogamy; in *Lamium*, for example, the spring and autumn flowers are cleistogamous, while the summer flowers are chasmogamous or sometimes cleistogamous in cold or rainy weather. In *Viola sepincola* the aerial flowers are chasmogamous in the sunshine and cleistogamous in the shade, indicating that light as well as heat may be a factor. The submersed flowers of *Alisma* also are cleistogamous.

Habitual cleistogamy is well illustrated by the subterranean and generally colorless flowers of *Viola cucullata* (and many other violets), *Amphicarpaea*, and *Polygala polygama* (fig. 497); in *Viola cucullata* they appear some weeks or months after the showy aerial flowers, but

[1] While *Yucca* is here considered as illustrating close-pollination, the moths, after gathering pollen, often fly to other flowers or even to other plants, so that they may effect autogamy, geitonogamy, or xenogamy.

in *Polygala* the two kinds of flowers are nearly synchronous. In all three cases they are much more productive than are the showy and presumably cross-pollinated aerial flowers. In the rock rose (*Helianthemum*) both the open and the closed flowers are aerial, the former being large and showy, while the latter appear later and are much smaller. In *Leersia oryzoides*, the conspicuous open monoclinous flowers rarely fruit, though the cleistogamous flowers hidden within the leaf sheaths are fertile. Few if any species have exclusively cleistogamous flowers, though this condition has been reported for *Myrmecodia echinata*, *Salvia cleistogama*, *Ophrys apifera*, *Ammannia latifolia*, and several grasses.

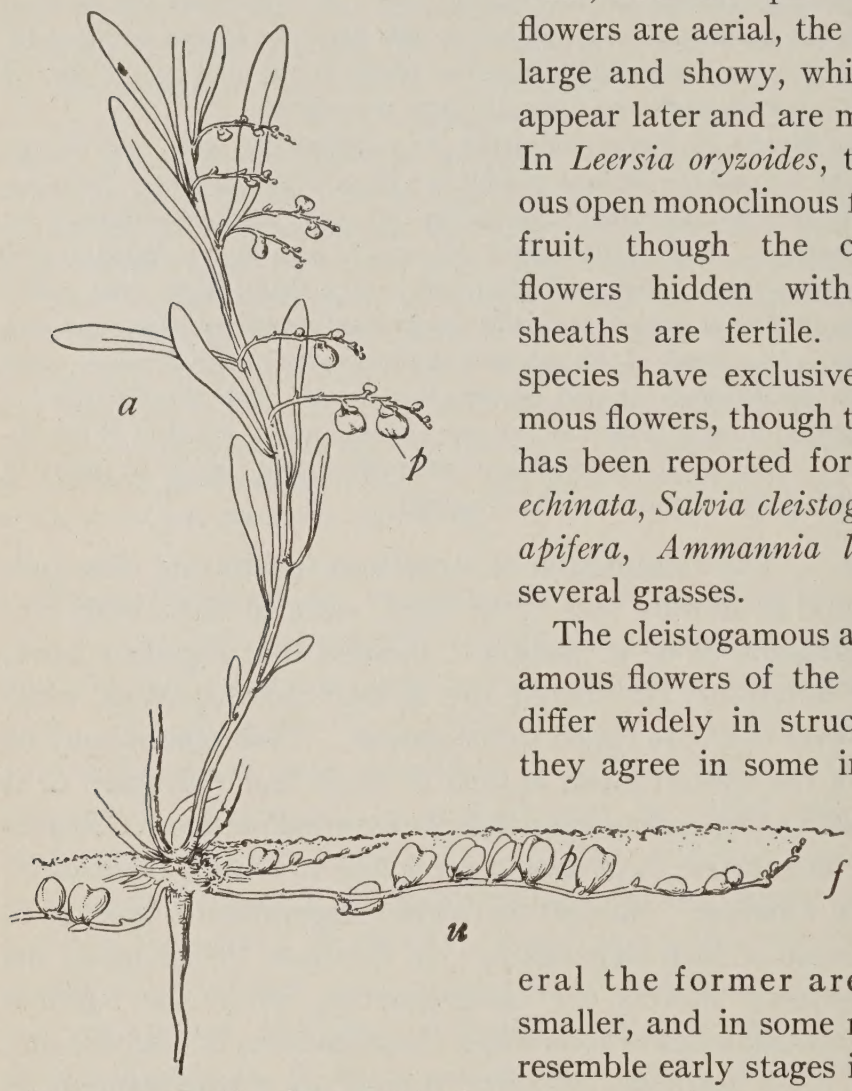


FIG. 497. — Fruiting shoots of *Polygala polygama*; the aerial stem (*a*) bears showy racemed flowers which open and may be cross pollinated; on underground stems (*u*) are borne numerous cleistogamous flowers (*f*), which are close pollinated and give rise to abundant seed pods (*p*).

The cleistogamous and chasmogamous flowers of the same species differ widely in structure, though they agree in some important respects as in the potency of own pollen. In general the former are much the smaller, and in some respects they resemble early stages in the development of the latter; this is especially true as to the corolla, which either is entirely lacking or exists in the form of protuberances (*e.g.* in *Specularia*), as in the bud of a chasmogamous flower. The development of the stamen and pistil is not arrested, as is that of the corolla, though the stamens may be fewer in number, and usually the pollen grains are much less numerous than in chasmogamous flowers. In *Helianthemum* the closed flowers have but three to ten stamens, as

contrasted with the numerous stamens of the open flowers; sometimes the stamens are reduced to a single anther, and the pollen grains may number only a dozen or even less in each chamber (as in *Oxalis*). Occasionally the pistil exhibits reduction; for example, in *Helianthemum* the open flowers have many ovules, while there are only a few in the closed flowers. Perhaps the most striking case of reduction is where, instead of a stigma, there is an open passageway to the ovules, recalling gymnosperms. Pollination, of course, is by direct contact, but there are some remarkable cases (as in *Oxalis* and *Impatiens*) in which, strictly speaking, there is no pollination at all, since the pollen grains germinate within the anther, putting forth their tubes which grow out toward the stigma.[1] In *Lamium* and in *Viola odorata* the anthers do not even dehisce, so that the pollen tubes have to penetrate the anther walls; in *Viola* the anther wall is devoid of the usual thickening, and the pollen tubes pass readily through permeable spots of small plasmatic cells. As might be expected, cleistogamous flowers do not exhibit marked dichogamy. Allied to cleistogamy is *bud pollination* (as in *Oenothera* and in various orchids), where autogamy occurs in ordinary flowers before they open.

The fact that the open flowers of plants which possess also cleistogamous flowers usually produce but few seeds has led to the theory that the failure of cross-pollination probably has resulted in the evolution of cleistogamy. This theory has no evidence in its favor. In *Viola biflora* there are cleistogamous flowers, although the showy open flowers fruit abundantly. Furthermore, close-pollination can take place quite as readily in the open as in the closed flowers of a given species, since own pollen is as potent in one case as in the other. As noted above (see also p. 416), cleistogamy is in part associated with arrested development, and usually is due to definite external conditions, which are unfavorable for chasmogamy; for example, in *Lamium amplexicaule* the first flowers in spring and the last flowers in autumn are cleistogamous, while the summer flowers are open and showy. Cleistogamy is advantageous in that closed flowers are well protected from rain and from the visits of pollen-gathering insects. Subterranean cleistogamy is advantageous in that the seeds are self-planted and are well-protected from many seed-eating animals, such as birds.

The comparative advantages of cross-pollination and close-pollination. — *Introductory remarks.* — Usually it is believed that cross-pollination must be highly advantageous because it is so common, and particularly that the diverse and sometimes extraordinary features which impede or even prevent close-pollination are *prima facie* evidence

[1] The germination of pollen grains within the anther has been reported occasionally even in chasmogamous flowers.

of the value of xenogamy. The usual reason for regarding cross-pollination as superior to close-pollination is either that it facilitates the merging of diverse racial characters[1] or that it promotes variability or racial vigor. The problem of cross-pollination is essentially a phase of the problem of sexuality, which has been considered previously.

Experimental data. — It long has been believed by plant breeders that occasionally crossing is necessary if the individuals of a species are to be kept in a state of the highest vigor, *inbreeding* (*i.e.* breeding between closely related forms, as in close-pollination) often having been shown to result in diminished luxuriance in the progeny. Careful experiments conducted many years ago on a number of species, though yielding rather discordant results, tended to show that cross-pollination, on the whole, is more advantageous than close-pollination. In some cases diminished vigor, which is made evident by smaller size and lessened seed production, is obvious in the progeny of the first generation (as in *Ipomoea purpurea* and *Mimulus luteus*); in a much larger number of cases it is obvious only after continued inbreeding for several generations, and in still other cases inbreeding appears never to result in deterioration.

Experiments made on Indian corn show that close-pollination results in the first generation in reduced height and yield; in the generations following there is further reduction, but the decrement becomes less each time until about the fifth generation, after which continued close-pollination makes no appreciable change in the offspring. Such dwarfs may reproduce as such indefinitely, but if crossed the offspring of the first generation has the original full size. In the earlier experiments geitonogamy usually resulted in quite as much weakening as did autogamy, showing conclusively that it is much more nearly related to close-pollination than to cross-pollination. Progeny from crossed individuals were found to flower first and to suffer less in crowded cultures than did progeny from inbred races; this fact has been taken to be of great significance, since it suggests the likelihood of the submergence of inbred races by cross-pollinated races in the " struggle for existence " in nature.

The possible advantages of cross-pollination. — The experiments cited may mean either that cross-pollination is in some way advantageous,

[1] If this conception is true, it still further emphasizes the essential difference between true cross-pollination and geitonogamy, since there is no such merging in the latter, the flowers of a single individual having a common immediate ancestry.

or that close-pollination is in some way disadvantageous. The supporters of the first theory have held that cross-pollination is advantageous, because it insures the mingling of two lines of ancestry with their supposedly different beneficial characters, or because it promotes variability or racial vigor. There is very little in favor of this view and very much against it. In the first place, experiments on the same species at different times and places vary widely in their results; sometimes own pollen may be quite impotent, sometimes imperfectly potent, and sometimes as potent as foreign pollen. Usually these variations are due to external factors, such as differences in moisture, light, etc. Many of the very species that have been supposed to demonstrate the benefits of cross-pollination grow under certain conditions quite as well when close-pollinated. Similarly, the results of cross-pollination vary widely under different external conditions. In case of crossing between unrelated individuals of inbred ancestry grown under similar external conditions, the progeny if grown under like conditions are scarcely more vigorous than with close-pollination, showing the vigor supposed to result from crossing may result rather from favorable external conditions. Comparable phenomena are known also in the animal kingdom.

The data from heterostyled plants oppose the usual theory of cross-pollination, since weak individuals or none at all result from crossing between plants with styles of unequal length, irrespective of nearness or remoteness of relationship; in such cases the progeny is weak, regardless of the mingling of " diverse racial characters." Dichogamy is cited as affording *a priori* evidence that cross-pollination must be beneficial, yet dioecious plants (in which close-pollination is of course impossible) exhibit the earlier maturation of anthers or of stigmas almost as habitually as do monoclinous plants.

The chief reasons for disbelieving that occasional cross-pollination is necessary in order to prevent the deterioration of plant species are afforded by the phenomena of autogamy and vegetative reproduction. Usually the argument for the value of cross-pollination is built on those cases in which foreign pollen is prepotent or own pollen impotent, omitting the equally numerous and significant cases where own pollen is fully potent. Apart from the vast number of plants that exhibit frequent autogamy, there are many in which autogamy is habitual, particularly the numerous species with cleistogamous flowers; in these there is no deterioration, in spite of repeated close-pollination. In the

experiments cited above, autogamy in several forms (as in *Petunia*, *Eschscholtzia*, and *Nicotiana*) resulted in progeny that was essentially as vigorous as when xenogamy was employed. Even in the two species (*viz. Ipomoea purpurea* and *Mimulus luteus*) which were thought most clearly to demonstrate the benefits of cross-pollination, luxuriant sports arose in the autogamous cultures, which had as vigorous progeny when close-pollinated as did cultures from cross-pollinated individuals. Perhaps most significant of all is the prevalence of vegetative reproduction in nearly all the higher plants. There is not a single case known in which the indefinite continuance of vegetative reproduction causes the slightest deterioration. Indeed, there are many plants in which crossing has essentially disappeared (as the duckweeds and the hornworts). Nor is there any evidence of deterioration in the species that are persistently parthenogenetic. It is to be noted that the plants which in experiments have shown benefit from crossing are chiefly garden varieties that have been much hybridized. No benefit from crossing has been shown in natural species that have long been pure. Nor is there good evidence that crossing promotes variability. Among the most variable of plants are the cleistogamous violets and such parthenogenetic genera as *Hieracium* and *Taraxacum*.

The possible disadvantages of close-pollination. — Even if there are no conspicuous advantages in cross-pollination, there may be disadvantages in close-pollination. Such a view seems particularly plausible in the case of those orchids in which own pollen seems to be prejudicial and possibly even poisonous to the stigma (or the stigma to the germinating own pollen), perhaps in a way analogous to the excreta of root hairs, except that here the deleterious effects concern only individuals of a species, and not the species as a whole. If this conception is valid, it may account for the occasional impotence of own pollen; in species where foreign pollen is prepotent, the deleterious influence of own pollen may be considered to be less marked. In the large number of species with potent own pollen it may be supposed that such deleterious effects are wanting. The benefits of cross-pollination and the disadvantages of close-pollination have been too much emphasized. Close-pollination and its essential equivalent, geitonogamy, are extremely common in nature, nor must it be forgotten, also, that many of the important plant and animal races utilized by man have reached their present state of commercial perfection by the most careful inbreeding.

The protective features of flowers. — *The calyx.* — Flowers are among the most delicate of plant organs, the ephemeral petals and the stamens and pistils with their gametophytes and embryos being particularly sensitive. Foremost among the protective organs is the *calyx* (fig. 442), which, during development, often is the only exposed floral organ, and commonly is much less delicate than are the structures it encloses. Among the dangers to which the developing corolla and the essential organs might otherwise be exposed are those arising from rain, drought, heat, cold, and wind.[1] Since the calyx commonly is composed of green and leaflike sepals, it probably plays an important part in food manufacture, as well as in protection, and occasionally it replaces the corolla in the matter of showiness. Sometimes bracts supplement or replace the calyx as protective structures, as in *Desmodium*. In the composites a calyx-like involucre is the chief protective organ (fig. 500). In the aroids the large spathe protects the entire inflorescence in flower as well as in bud. Even the corolla may be a protective organ, as in the grape, where it falls as soon as the bud opens, and in flowers which close at night and in stormy weather.

The duration of flowers. — From the standpoint of protection, flowers may be divided into those that remain open throughout anthesis and those that close once or more during that period. Of those which remain open, many are ephemeral, and hence need but little protection, particularly as opening usually comes only in favorable (*i.e.* warm and sunny) weather. Among the latter are the flower-of-an-hour (*Hibiscus trionum*), which has the most ephemeral of flowers, rarely lasting for more than three hours, the day lily (*Hemerocallis fulva*), and the night-blooming cereus. In striking contrast with these are certain orchid flowers which may remain open for fifty to eighty days if unpollinated (as in *Odontoglossum*).[2] On the whole, plants with ephemeral flowers are more likely to have a large number of blossoms in a season than are plants with long-lived flowers.

The protection of non-closing flowers. — Long-lived, non-closing flowers would seem to need some protection, the greatest dangers, perhaps, being the waste of pollen through rain, the drying of the stigmatic surface through drought, and injury from low temperature or frost.

[1] An illustration of calyx protection is afforded by the peach and strawberry, in which unopened buds are much less subject to injury from frost than are buds that are partly or fully opened.

[2] The early withering of orchid corollas may be induced not only by pollination, but also by the mechanical irritation of the stigma.

Pollen is not readily wetted, which is itself a matter of considerable protective importance; also it will be recalled that some pollen, such as that of exposed vernal flowers, is not readily injured by wetting or by low temperature. Many plants have nodding flowers, notably the ericads, and also *Bryophyllum* and *Yucca* (fig. 498), and thus are well

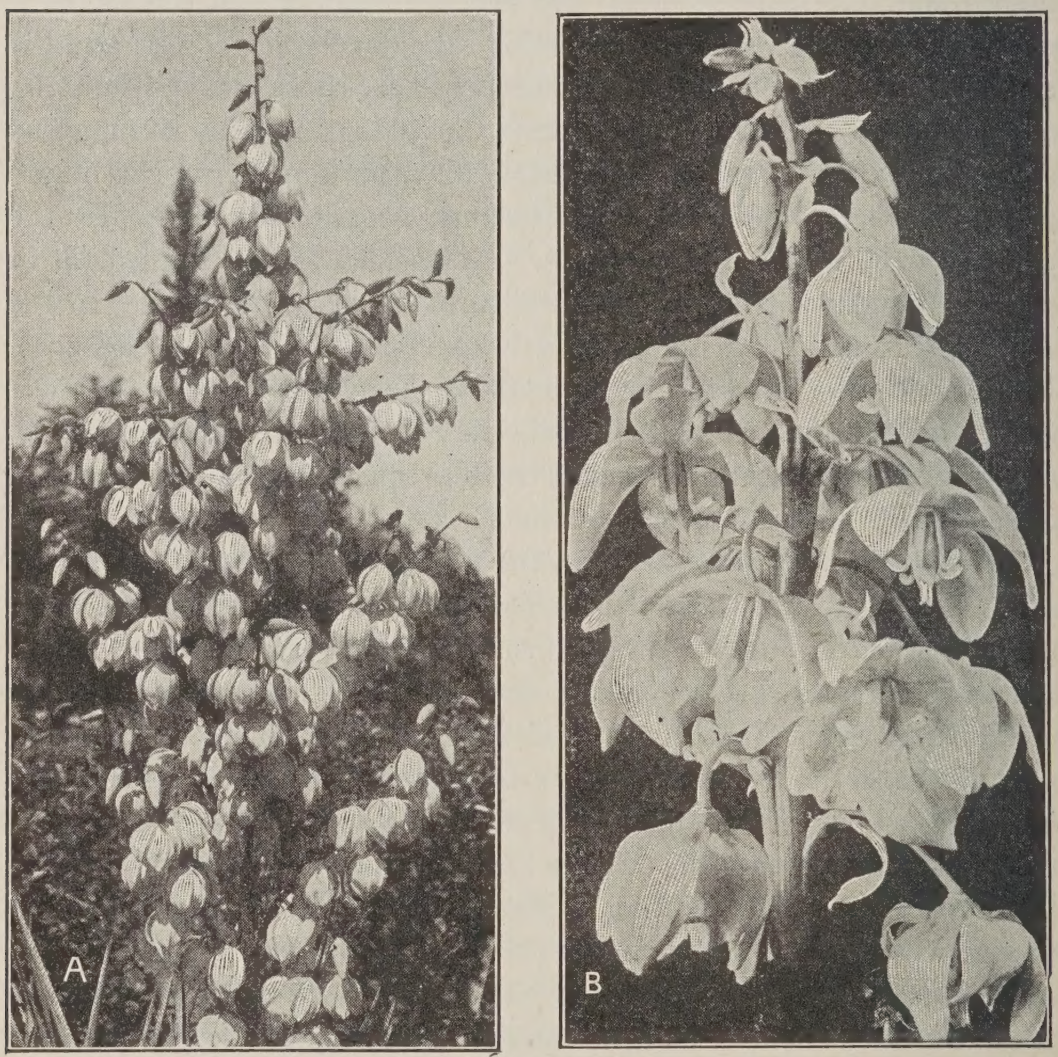
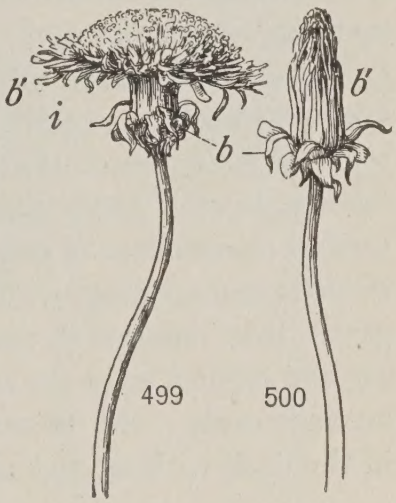


FIG. 498. — *Yucca* flowers: A, an inflorescence of *Yucca patens* with numerous pendulous flowers; B, flowers of *Yucca treculeana;* note the perianth, the stamens with recurved anthers, and the stigmas. — From TRELEASE.

protected from injury by rain. Many of the features that protect flowers from crawling insects also protect them from rain; among these are contracted corolla throats (as in *Arctostaphylos* and in various borages), and zygomorphic corollas, which not only are more or less closed, but commonly are swung laterally, as in the labiates (fig. 480) and in the orchids.

The protection of flowers by closing. — Closure during anthesis usually involves a single flower, but sometimes it involves an entire inflorescence, as in the heads of the milky-juiced composites (figs. 499, 500). Most such flowers or inflorescences open in sunshine and close at night and in cloudy weather, though in a few cases this order is reversed, the flowers opening at night and in cloudy weather and closing in the sunshine. Some flowers open for two successive days (as in the poppy), others for three to five days (as in *Eschscholtzia*); the flowers of *Crocus* and *Hepatica* may open daily for more than a week. Usually nocturnal flowers are more ephemeral than are diurnal flowers (as in the night-blooming cereus), but the flowers of evening primroses, although opening but once, remain open for some hours after sunrise; the flowers of some species of *Silene* open for at least three successive nights. Flowers often have a longer period of anthesis in spring and autumn than in summer; even such ephemeral flowers as those of *Hibiscus trionum* and *Hemerocallis fulva* may open toward the beginning or the end of the flowering period on three successive days.



FIGS. 499, 500. — Floral opening and closing in the dandelion (*Taraxacum officinale*): 499, an open head as seen in full sunlight; 500, the same head as seen at night; the involucre (*i*) is double, consisting of short outer bracts (*b*) and a single row of long inner bracts (*b'*); opening and closing are due chiefly to the movements of the inner bracts, the position of the outer bracts shifting but slightly.

Flowers cannot be classed simply as diurnal or nocturnal, since most hours of the day and night are marked by the opening or closing of the flowers of some species. The opening and the closing hours of a given species vary widely with the latitude and the season, but in general the earlier diurnal flowers open about sunrise (as in the chicory and the morning glory) and the latter about noon (as in the *Mesembrianthemum*). The nocturnal series begins about dusk (as in *Silene*) and closes about ten (as in *Cereus*). The times of closing are much less definite than are those of opening, and they extend over most of the twenty-four hours; this is partly because flowers open much more rapidly than they close, the former process sometimes being sudden, as in *Oenothera*. Beginning with the early forenoon (as in salsify and chicory) each hour until after sunset is marked by the closing of some diurnal flowers. Similarly nocturnal flowers may close at any time from midnight (as in *Cereus*) to sunrise, or even during the following forenoon (as in the evening primrose). The entire scheme, as above outlined, may be disarranged in cloudy weather.

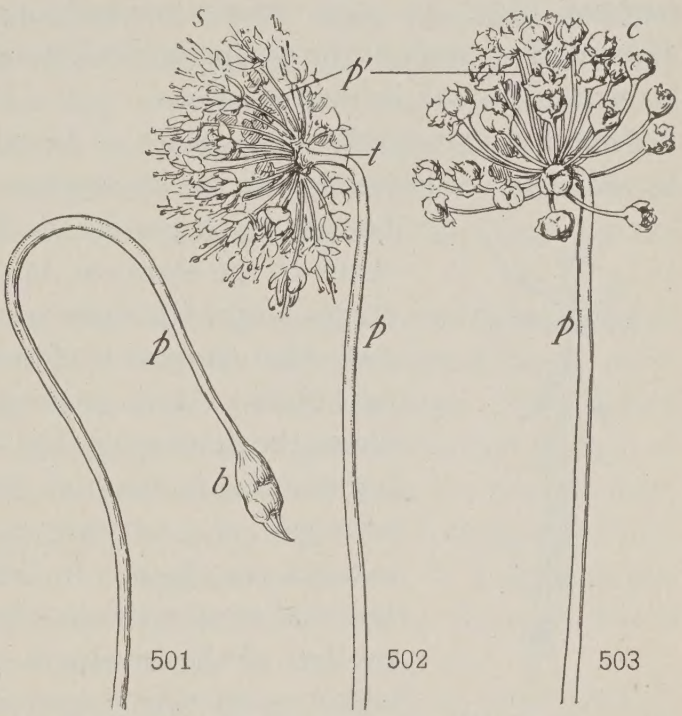
The factors involved in the opening and the closing of flowers. — The mechanism of opening and closing and the factors controlling this mechanism are in part unknown. It has been shown in a few cases, and it is believed to be true in others, that these movements are true movements of growth, opening being due to epinasty, and closing to hyponasty, in the segments of the perianth or involucre. Probably the chief single factor causing epinasty, and hence opening, is an increase of temperature. Opening as a result of an increase of temperature has been proven experimentally in a number of cases, notably in the tulip and the crocus; a crocus flower opens in two to four minutes, when the temperature is raised suddenly fifteen or twenty degrees, and it is sensitive to a change of half a degree. Successive alternations of cold and warmth may induce several successive closings and openings within an hour. It is believed by many investigators that changes in turgor are responsible for some cases of opening and closing, as in the tulip. Possibly some flowers open and close autonomously; the flowers of *Calendula arvensis*, for example, open in the dark without any change in temperature.

In some cases light, independently of temperature, has been shown to cause opening (as in the day lily and in the gentians). In nature both light and heat probably coöperate, especially in opening; the early closing of far northern flowers, in spite of long daylight, probably is a matter of temperature alone. In a few cases opening and closing are due to moisture changes; so sensitive is the head of *Carlina* to such changes that it has been used as a hygroscope, closing in moist air and opening in dry air. Obviously the explanation of the movements of flowers that do not open rather promptly at sunrise or close at sunset presents certain difficulties. While these have not as yet been solved experimentally, it is likely that certain species require a greater amount of heat or light for opening or a less amount for closing than do others, or that they are less quickly sensitive. Most remarkable are the nocturnal flowers, in which opening is caused by decreased temperature and light instead of by increased temperature and light, as in diurnal flowers.

The advantages of flower closing. — In general, flowers that close during anthesis are open at the time when their special pollinating insects are most active. Most of the latter (especially the bees and butterflies) are diurnal, and are affected by the same factors that influence flower opening, such as increased heat and light and low atmospheric humidity (or at least absence of rain). Nocturnal flowers are pollinated almost exclusively by nocturnal insects, such as certain moths. How such a remarkable correlation of flower opening and insect activity may have arisen is altogether unknown. It is probable

that closure when the insects are not active is likely to be of considerable protective importance; in diurnal flowers pollen probably is conserved by closure in rainy weather, and in all cases closure for a part of the time would seem to favor the lengthening of the period of stigmatic receptivity, particularly in nocturnal flowers, which are freed from the desiccating influence of sunlight. In addition, as previously noted, opening and closing favor close-pollination and even geitonogamy in the composites.

Protective movements other than floral opening and closing. — In some flowers the anther valves are hygroscopic (as in *Alchemilla* and *Laurus*), closing in moist weather; usually they are closed much more quickly than the closure of perianth segments is effected by low temperature, a few seconds commonly sufficing. Such closure is of direct value in protecting pollen from rain. It may be recalled, also, that in anthers, dehiscence generally is caused by desiccation, so that the first opening is unlikely to occur in wet weather. Many plants show movements of the flower axes (*pedicels*) or inflorescence axes (*peduncles*). In certain instances the buds are erect and the flowers pendent (as in *Aquilegia*). More closely related to floral movements are those cases in which the flower is erect by day and pendent by night and in rainy weather (as in *Geranium* and *Anemone*); in the umbellifers there is a similar movement of the entire inflorescence. Such movements are due to growth



FIGS. 501–503. — Growth movements accompanying flower and fruit development in a wild onion (*Allium cernuum*): 501, a flower bud, showing the nodding position of the young peduncle (*p*); *b*, spathe; 502, a shoot in full bloom; note that the peduncle (*p*) has straightened out except at the tip (*t*); the flowers are arranged in an umbel, the pedicels (*p'*) being oriented in various directions; note the exserted stamens (*s*); 503, a shoot in fruit, showing the conspicuous capsules (*c*); note that the pedicels (*p'*) have become erect or ascending.

inequalities in the pedicels or the peduncles, and the advantages therefrom would appear to be in exposure to pollinating insects in sunshine, and in protection from rain and cold during the night or in rainy weather. In the poppy the buds are nodding, but the flowers are erect, the pedicels becoming apogeotropic. Movements of much complexity, but without obvious advantages, are seen in *Allium cernuum* (figs. 501–503), where the nodding bud becomes erect by differential growth in the peduncle, while later the fruits become erect by similar growth in the pedicels.

Protection during fruit development. — Usually the developing ovules are delicate. Ultimately the enveloping ovary walls and seed coats become thick protective structures of considerable value to the embryos, but often during the earlier stages of growth some protection from desiccation and other dangers is afforded by special structures or habits. After anthesis the calyx may close about the developing fruits (as in *Physalis*), appearing much as in the bud, thus once more serving as an organ of protection, as well as continuing to manufacture food. In the composites the protective and synthetic activity of the calyx is replaced by that of the involucre. Many fruits which are edible when ripe, during immaturity are more or less protected from predatory animals by unpleasant flavors, hardness, and spinescence (as in *Opuntia* and *Ribes*), and perhaps by inconspicuousness, since their green color is similar to that of the leaves.

FIG. 504. — A flowering spike of the lopseed (*Phryma leptostachya*); at anthesis the flowers (*f*) with their bilabiate corollas (*c*) are horizontal, but subsequent epinastic growth causes the fruits (*f'*) to become strongly reflexed.

In many plants, especially in hydrophytes, the developing fruit-stalks exhibit striking growth curvatures. In most cases the previously erect stalk recurves (as in *Peltandra* and *Nymphaea*), causing the downward orientation and consequent submergence of the fruit. Some land plants show similar reactions, notably *Phryma* (fig. 504), whose fruits become strongly reflexed, whence the common name, lopseed; in the peanut, stalks that are erect or ascending until anthesis, later recurve and force the developing nut into the ground. Probably in all of the above cases pedicels or peduncles originally apogeotropic become progeotropic after anthesis, but no explanation

of such peculiar behavior has been given, nor is there any obvious advantage, except perhaps a slight one, in connection with planting (p. 444).

The origin of floral structures. — The flower is the most complicated of plant structures, and the organs concerned directly or indirectly with pollination form the most complicated part of the flower. An adequate theory of flower structure, however, must explain not alone this complexity, but also the evolution of the mouth parts of the flower-visiting insects (notably those of the bees, butterflies, and moths), which appear to be so obviously related to the flowers. Capping all, and most difficult of all to explain, are the cases of obligate reciprocal symbiosis, of which the fig and the yucca are the most remarkable.

Since the abandonment of the theory of special creation, a common hypothesis has been that floral structures and specialized mouth parts have arisen *pari passu* by reciprocal natural selection. This theory implies that those flowers and insects of each generation that happen to exhibit the greatest reciprocal specialization will be the ones to have progeny, while the more generalized forms will be so handicapped that they will be submerged in the " struggle for existence." Upon analysis this theory seems almost inconceivable; furthermore, there are few if any facts to support it, and many facts to controvert it.

In the first place, many floral features, such as the kind of inflorescence, the position of the various organs, the forms and markings of the corolla, and the association of dichogamy with dioecism, have no known advantage, much less an advantage great enough to make their possessors better adapted than are their neighbors.[1] Nor is there the remotest evidence that generalized flowers are less successful than those that are specialized. Indeed, the orchids, which have the most specialized of flowers, appear to be on the way toward extinction, because of this very specialization; they represent a case of " over-adaptation," and therefore present a condition that is contrary to the fundamental postulates of natural selection. In some other groups of plants the flowers are so strongly protandrous that pollination rarely takes place, because insect visits occur either after the pollen is shed or before the stigmas mature. In contrast to the orchids, the grasses and the catkin-bearing trees are dominant and widely successful groups of

[1] The association of protandry and geitonogamy, which is very common in the composites, would also seem to be without advantage.

plants, although they possess generalized flowers, which are diclinous and wind-pollinated.

Actinomorphic flowers with exposed pollen and nectar often are visited in preference to long-tubed or zygomorphic flowers, even by such specialized insects as the bees, and it has been noted that the former usually set seed more regularly than do the latter. That dichogamy is not due to natural selection seems to be indicated by the fact that often it is modified by external factors; for example, in the sunshine the flowers of *Parnassia* are protandrous and those of *Biscutella* and *Thlaspi* are protogynous, but all alike become homogamous in the shade or in cloudy weather. In many cases the postulated intimate and exact relation between a specific insect and a specific flower may well be doubted for a number of reasons: the same flowers are pollinated by very different insects in different countries; naturalized flowers seem to be pollinated by the insects of the new country quite as successfully as their congeners are pollinated by the insects of their native country; insects sometimes are held captive and even are killed by specialized floral structures, as in *Asclepias* and *Hedychium;* bees that are unable to reach the honey in long floral spurs frequently bite holes at the side, thus getting the nectar without effecting pollination.

Probably the chief reason for not holding to natural selection as a factor of prominence in the origin of floral structures is that flowers, though they are the most diversified and specialized of plant organs, probably have played a comparatively minor rôle in determining the success of plant groups. It is likely that the success of the grasses and the catkin-bearing trees is due less to the floral features above noted than to vegetative reproduction in the former and to the tree habit in the latter.

Perhaps the best evidence in support of the view that flowers contribute largely to the success of plants is found in the composites, though even here it is likely that vegetative reproduction and the wind dispersal of seeds play a larger part. Even the composite flower owes its advantage not so much to floral specialization as to the massing of inconspicuous and relatively non-specialized flowers into compact heads, which greatly facilitates pollination. Furthermore, it is to be remembered that the composites, forming supposedly the highest of plant groups and certainly the largest in number of species and one of the largest in display of individuals, are notable for their geitonogamy and autogamy, for their relatively actinomorphic flowers (the disk

flowers being strictly actinomorphic) with their pollen exposed for any insects that may visit them, and for their tendency toward dicliny; it may be significant, also, that the greatest display of parthenogenesis among seed plants is among the composites.

The preceding paragraphs appear to show that the fundamental postulate of natural selection, namely, that the trend of evolution is along the line of maximum advantage, is untenable, at least so far as flowers are concerned. The evolution of the orchids beyond the point of maximum advantage, the phenomenal success of the groups with generalized flowers, and the probable dominance of the vegetative over the reproductive factors in determining success in the majority of groups, all appear to indicate that some other factor than natural selection has determined the diversity of floral structures. Though the theory of natural selection seems to explain such structures quite as inadequately as did the old and discredited theory of special creation, it is not possible as yet to put one which is adequate in its place. Perhaps the most tenable theory is that of orthogenesis. This theory postulates a definite trend in the course of evolution, regardless of the influence of selection. It would assume that the specialized features of flowers and also of insects are organization characters that are more or less inherent in the species. According to this conception the insects and flowers are not adapted to each other, but insects in their floral visits select those flowers whose structures happen to be suited to their mouth parts. It is obvious that this still leaves unanswered the most fundamental question of all, namely, the cause of floral structures. In the present state of knowledge, it is not possible to say whether the evolution of floral structures has been determined chiefly by external factors or by factors that we call internal. This subject, in so far as it has to do with external factors, belongs properly to the following section.

3. THE INFLUENCE OF EXTERNAL FACTORS UPON THE DEVELOPMENT AND FORM OF REPRODUCTIVE ORGANS

Introductory remarks. — Variations in the development and form of reproductive organs are less common than are similar variations in vegetative organs, but they are much more common than has been supposed. Their relative invariability has long made differences in reproductive structures the chief basis of classification. For this very reason

variation is nowhere more significant, since, if the present theories of classification are correct, the study of reproductive variations, however few or inevident they prove to be, may lead to the interpretation of evolution. The possibilities of experimentation in this field are well shown by a study of the fungus, *Saprolegnia;* from a single mycelium there have been derived by appropriate changes in the media the forms of asexual reproduction that have been held to be characteristic of six different genera.

Reproductive variation in the seedless plants. — *Experimental data from the algae and the fungi.* — In the seed plants it is common to speak of two contrasting states, namely, the vegetative and the reproductive, but in many algae there are three such states, characterized respectively by vegetative activity, by asexual reproduction, and by sexual reproduction. It is believed that the inception of each of these states depends upon definite external factors, though vegetative activity necessarily must antedate the others, since it is the stage of food accumulation.

Vegetative activity may be prolonged indefinitely, being favored by the continued uniformity of optimum vegetative conditions. The most important single factor favoring such activity appears to be the constant presence of sufficient water to keep the cell sap dilute, and to facilitate active growth. Another important factor seems to be a uniform and moderately high temperature, chiefly, perhaps, because of its effect upon the absorption of water. Under uniformly high temperatures, *Bacillus anthracis* and other bacteria have been kept in a state of continued vegetative activity, with no tendency to develop resting cells (" spores "). *Saprolegnia* has been kept for six years in a purely vegetative condition, and brewers' yeast probably has been kept essentially vegetative for centuries.

Both sexual reproduction and asexual reproduction are induced by changes in external conditions, and particularly by changes that are detrimental to optimum vegetative activity. Although species differ quantitatively and qualitatively as to the precise external factors that are involved in the initiation of reproductive activity, it has been shown in many cases that the development of reproductive structures is induced by desiccation, by increased concentration of the medium, by very high and by very low temperatures, by intense illumination, by decreased food supply, and by the presence or absence of specific chemical substances. It is scarcely possible as yet to distinguish sets

of factors which commonly initiate sexual reproduction as opposed to asexual reproduction, although in some cases (notably in the molds) the development of asexual spores is favored by those factors which are most opposed to vegetative activity, namely, desiccation, food impoverishment, low temperature, high concentration of the medium, and strong illumination; zygospore formation, on the other hand, is favored in the molds by conditions which more closely resemble those favoring vegetative activity, namely, moisture, rich food supply, high temperature, low concentration of the medium, and darkness. However, sexual reproduction is favored by strong illumination in *Vaucheria*, by low temperature, and by food impoverishment in *Saprolegnia*, and by desiccation in *Spirogyra*. In some cases it seems as if almost any alteration of previous conditions serves to initiate reproductive activity, and in other cases there seem to be certain individuals or strains predisposed to continued vegetative activity, while other individuals or strains appear to develop reproductive organs, almost regardless of external conditions. From the reproductive standpoint one of the most plastic of plants is *Vaucheria*, which in poorly illuminated running water may be kept in a vegetative condition for several years, while in standing water it produces zoospores if weakly illuminated, and sex organs if well-illuminated or if grown in media poor in food;[1] zoospores may be formed also when the food is scanty, and desiccation may result in the formation of non-motile, thick-walled resting spores (aplanospores).

In the lichens shade and moisture favor the formation of the soredia, while light and desiccation favor the development of the organs concerned in asexual reproduction (*apothecia*). In *Botrydium*, zoospores develop in water, but when the plants are desiccated, there develop aplanospores comparable to those of *Vaucheria*. *Saprolegnia* is quite as plastic as is *Vaucheria*, vegetating indefinitely if well nourished, but developing zoospores if grown in distilled water; the development of sex organs is favored by growth on solid substrata, by low temperatures, by food impoverishment, and by the addition of specific salts to the media. In *Spirogyra* zygospore formation is facilitated by high temperature as well as by desiccation; there is a striking contrast between the dark green vegetative filaments of dilute fresh water and the yellowish reproductive filaments of ponds that are drying up. In *Oedogonium*, zoospore production is favored by depriving the media of nitrates and phosphates, by growth in darkened distilled water, and by transfer from a rich to a poor nutrient solution. In *Botrytis* there is a reciprocal relation between the sclerotia and the conidia, the former being favored by good vegetative conditions,

[1] In *Hydrodictyon* intense light favors zoospore production, and in *Ulothrix* light seems to be without influence in this connection.

while spore formation is favored by desiccation, by poor nutrition, and by high concentration of the medium. Species differ widely as to the effect of increased concentration of the medium; in *Stigeoclonium*, and perhaps in most forms, low concentrations favor zoospore production, but in *Tetraspora*, zoospores continue to develop at high concentrations, and in *Vaucheria*, concentration seems to make but little difference. In *Basidiobolus* low concentrations favor zygospore production, and high concentrations facilitate the development of thick-walled resting spores. A reduced supply of oxygen appears to induce reproduction in *Ulothrix*. *Monas*, one of the infusorians, reproduces vegetatively or sexually at 20° C., but by asexual spores at temperatures between 1° C. and 4° C.

Comparatively little is known concerning reproductive reactions to external conditions among the higher fungi, though in *Coprinus*, *Stereum*, and *Xylaria* reproductive activity is favored by illumination, by poor nutrition, and by partial desiccation. In the rusts the development of teleutospores is hastened by refrigeration, as in alpine cultures. It has been found also that in *Uromyces veratri*, similar aecidiospores produce the uredo generation if sown on young leaves, and the teleuto generation if sown on old or wounded leaves, suggesting that the kind of spore that is formed may be related to nutrition. In some cases external factors not only initiate periods of reproductive activity, but they influence the character of the reproductive structures; for example, in some of the rusts the spore walls are thicker in xerophytic situations than elsewhere, and in *Bornetina* the size, shape, and sculpturing of the spores vary with the culture media and with the illumination.

In certain marine algae, as *Dictyota dichotoma*, there is a remarkable periodicity, which seems to be related to external conditions. In England the sex organs develop at fortnightly periods, the gametes being liberated at a fixed interval after the highest spring tide. In North Carolina there also is a relation to the tides, but the production of sex organs occurs monthly rather than fortnightly. Similar phenomena have been observed at Naples, and in Japan a fortnightly period of gamete liberation has been discovered for *Sargassum*. The most probable causative stimulus of reproductive periodicity is the increased illumination that is associated with the fortnightly recurrence of extreme low water; at Naples the liberation of gametes appears to be on the day when low water occurs nearest to midday. Factors which modify the tides, such as wind or change of atmospheric pressure, also affect the time of gamete liberation.

The influence of external factors upon reproductive activity in animals appears to be much less obvious than in plants. However, in *Paramecium* and in other infusorians the continuance of favorable nutritive conditions seems to cause continued vegetative activity, whereas conjugation is due chiefly to changes in the media. In the water fleas (*Daphnia*) there are two kinds of generations, one being composed of males and females, and the other being composed solely of parthenogenetic females. It has been ascertained that parthenogenetic generations result when the conditions for nutrition are favorable, whereas bisexual generations result from conditions unfavorable for nutrition, such as increased concentration of the medium, desiccation, high or low temperature, the accumulation of excreta, and starvation. In nature the bisexual generation is especially to be seen in shallow pools, and in autumn in ordinary ponds. The conditions for the development of parthenogenetic and bisexual generations are very similar in certain other animals,

such as rotifers (*Hydatina*), plant lice (aphids), and the grape-louse (*Phylloxera*). Under favorable nutrient conditions there may be many successive parthenogenetic generations without any intervening bisexual generations.

The origin of sexuality. — There is little experimental evidence bearing upon the origin of sexuality, although there exist a number of forms with facultative gametes, and even with facultative gamete-producing organs (gametangia). In *Ulothrix* (figs. 439, 440) there are intergradations (*e.g.* zoospores of intermediate size with two or four cilia) between the large quadriciliate zoospores and the small biciliate gametes, suggesting the possible origin of gametes from zoospores; indeed, it is known that without fusion gametes sometimes develop into plants, quite as do zoospores. In *Hydrodictyon* similar primordia produce gametes in some media and zoospores in others. In *Zygnema stellinum* there are intergradations between the isogamous, the heterogamous, and the parthenogenetic gametes, and in the sea lettuces, *Ulva* and *Enteromorpha*, there are small conjugating gametes and large parthenogenetic gametes. The auxospores of diatoms may develop vegetatively, may form asexual spores, or may conjugate sexually. In *Ectocarpus* there are transitions between sporangia and gametangia, the same structures producing either zoospores or isogamous or heterogamous gametes, thus suggesting the possible origin of sex as well as of sexuality. In all of these cases the exact determinative factors remain to be discovered, although it has been suggested from their small size in comparison with zoospores and parthenogentic gametes that conjugating gametes represent poorly nourished spores.

Artificial parthenogenesis. — The most important experimental evidence concerning parthenogenesis is derived from animals, and in view of its great significance, it must be cited here. Parthenogenesis is observed somewhat frequently in a number of animals, such as bees, wasps, and plant lice; in the latter it occurs especially at high temperatures or when the host plant is very watery. It has been demonstrated that the eggs of the sea urchin (*Arbacia*) develop into larvae in the absence of sperms, if they are placed in somewhat concentrated solutions of magnesium chloride and sea water. Comparable results were obtained with other salts, and all were at first referred to the increased osmotic pressure occasioned by their presence. Hence it was suggested that the stimulus necessary for egg development is the extraction of water. Later experiments have demonstrated that artificial parthenogenesis can be brought about in many other ways than

by exposing eggs to increased osmotic pressure, and it is becoming evident that the explanation of the process is by no means simple; a feature of recent experiments is the emphasis that has been placed upon chemical factors.

Experiments with similar results have been made upon the eggs of other echinoderms than the sea urchin (*e.g.* those of the starfish, *Asterias*), and also those of certain annelids (as *Chaetopterus* and *Polynoë*) and mollusks (as *Sottia*). In the starfish, eggs develop parthenogenetically when they are exposed for several hours to temperatures below 7° C. It was found some time ago that the eggs of *Chaetopterus* develop parthenogenetically by the addition to the medium of potassium ions in an amount too small to produce an osmotic effect, and more recently various acids and alkalis have been seen to act similarly. Treatment with a fatty acid (as acetic acid) before placing in a concentrated solution greatly stimulates development, because it causes the formation of a membrane, just as when a sperm fuses with the egg. The mechanical agitation of eggs sometimes causes their parthenogenetic development. Indeed it would seem that almost any disturbance may serve to stimulate the development of certain eggs. Probably a large factor in the case is the permeability of the egg to the substances it needs for its development, and it may be that the various stimulating influences have as their chief rôle the establishment of increased permeability. In most cases artificially parthenogenetic animals die in an early stage of development, but in at least one instance mature sea urchins have been secured by this means.

Few similar experiments have been performed with plant eggs, though parthenogenesis has been induced in *Spirogyra* and in *Chlamydomonas* by growing plants in concentrated (6 per cent) solutions of cane sugar; in these experiments plasmolysis occurred, indicating the extraction of water, as in *Arbacia*. Artificial parthenogenesis has been reported for other plants, such as *Protosiphon* and *Marsilea*, high temperature seeming to be the stimulating factor. The experiments on artificial parthenogenesis seem to suggest that the rôle of the sperm is less that of a carrier of necessary hereditary substance than that of a growth excitant, which by physical or chemical means makes the egg permeable to the substances which bring about development.

Sexuality in the fungi. — The sexual relations of the fungi are very suggestive of modifications resulting from saprophytic or parasitic modes of life, although confirmatory experimental evidence is largely lacking. In *Saprolegnia* and *Achlya* there are all gradations between completely developed male sexual organs and the absence of such organs. Some forms have apparently complete sexual organs but the eggs develop parthenogenetically; other forms have antheridial tubes which reach the egg but remain closed or merely pierce the oogonium

wall without reaching the egg; still other forms have no antheridial tube, and some forms have no antheridium. There may be considerable variation also within a given species; for example, antheridia are rarely present in *Saprolegnia thureti*, as often absent as present in *S. mixta*, and usually present in *S. hypogyna;* they are always present in *S. monica*. In no case are the female organs absent, so that *Saprolegnia* forms a striking instance of parthenogenesis by reduction.[1] In the zygomycetes there are gradations between heterogamy and isogamy, suggesting the evolution of the latter from the former by reduction, and in the ascomycetes there appear to exist many stages in the reduction of sexuality. In comparatively few fungi does there appear to be a fusion of ordinary gametes, though a number of apparently modified forms of sexuality have been discovered in the rusts and smuts and in certain other groups. Even the formation of asexual spores appears to have ceased in some fungi, as in the internal fungus of *Lolium*, which probably is a smut, and it is rare in others, as in most mycorhiza fungi. It commonly has been supposed that the reduced or modified sexuality of the fungi is in some way associated with their saprophytic or parasitic mode of life; since well-nourished plants reproduce sexually less than do poorly nourished plants, it is possible that the good nutritive conditions of the group in part account for the character of its sexual development.

Reproductive variations in the bryophytes and pteridophytes. — Light favors the development of sex organs in liverworts, mosses, and ferns. In *Marchantia*, weak light or an excess of moisture favors ordinary vegetative reproduction; an increase of illumination favors the development of gemmae, and strong illumination favors the development of sex organs. In weak light, fern gametophytes develop into filaments resembling moss protonemata instead of producing sex organs. If in *Salvinia* the sperms and eggs fail to fuse, the female gametophyte, whose growth commonly is checked at such fusion, continues to grow vegetatively, producing new female organs; thus embryo development seems in some way to check gametophytic vegetative activity. Similarly, the gametophytes of *Osmunda* are long-lived, if fusion does not take place. While most fern gametophytes are monoecious, producing first male organs and then female organs, gametophytes that are

[1] Cases of reduction are known also in animals; for example, some rotifers have small and functionless males or none at all, and in some crustaceans (as *Limnadia hermanni*) and ostracods (as *Cypris reptans*) only females are known, though they still retain the sperm sac.

poorly nourished (having, for example, a small supply of nitrogen) or are exposed to strong illumination, may produce male organs only, as though the food supply were insufficient for complete development; in rare instances, vigorous, well-nourished gametophytes bear only archegonia. In the ostrich fern (*Onoclea struthiopteris*) the gametophytes commonly are dioecious, the larger plants being female, and the smaller plants being male; in ordinary cultures one to twelve per cent of the plants are monoecious. Under certain culture conditions, as when female plants are transferred to rich nutrient media, at least fifty per cent of the plants may become monoecious. Similar phenomena occur in some monoecious mosses, antheridia being the only sex organs developed when the nutritive conditions are poor; in some dioecious forms (as in *Dicranum*) the male plants are smaller than the female plants. In the ferns it often is easy to induce apogamy and apospory, especially where the illumination is weak, or where the soil is dry or poor in food materials.

A somewhat remarkable situation occurs in *Equisetum;* though it is a homosporous genus, some of its ancestral relatives were heterosporous, and even now the gametophytes usually are dioecious, though arising from approximately similar spores. However, the smaller and more poorly nourished gametophytes usually bear male organs and the larger gametophytes, female organs. Furthermore, the smaller spores are likely to give rise to male gametophytes and the larger spores to female gametophytes; in the true ferns, however, there appears to be no relation between the size of the spore and the sex of the gametophyte that comes from it. Occasionally, the gametophytes are monoecious, the female organs appearing last, as in ordinary ferns. In *Marsilea*, one of the heterosporous pteridophytes, the development of fruiting organs (sporocarps) may be incited by partial desiccation (as in the drying up of a pond), by increased illumination, or by high temperature; on the other hand, fruiting may be retarded or prevented by placing the plants under water in weak light, at low temperatures, or in crowded cultures. In the microsporangia there are sixty-four primordia which develop commonly into microspores, but of the sixty-four megaspore primordia, only one develops, and that at the expense of the others nutritively. It has been shown that by subjecting developing *Marsilea* sporocarps to spraying by cold water, no megaspore primordia develop, but that structures resembling megaspores may be made to develop from microspore primordia

under optimum nutritive conditions, growth being at the expense of other primordia, as in the development of ordinary megasporangia; sometimes such spores are sixteen times as large as ordinary microspores. Thus it is suggested that heterospory may have arisen from homospory through the influence of optimum nutrition on developing sporangia.

Some ferns show interesting transformations of reproductive primordia into vegetative organs; for example, in *Osmunda* and *Botrychium* there often are leafy organs in the reproductive region, and in *Onoclea* the removal of the foliage leaf is followed by the development of another foliage leaf from the primordium of the reproductive shoot.

Reproductive variations in the seed plants. — *Vegetative and reproductive periods.* — In the seed plants it is convenient to distinguish as the reproductive phase all of the complex phenomena, both sporophytic and gametophytic, from the inception of the flower to the maturation of the seed, contrasting this with the vegetative phase of the sporophyte. As in the lower plants, a vegetative period always antedates the period of reproduction. The length of this initial vegetative period differs widely, varying from a few weeks in certain xerophytic annuals to a number of years in the century plant and in most trees. There may be but one reproductive period following this initial vegetative period, as in annuals and biennials, and in such perennials as the century plant; in these forms, which are known as *monocarpic* plants, death follows fruit maturation. In most perennials, however, reproduction either continues indefinitely after its inception or more often recurs at certain periods, vegetative activity also continuing indefinitely or periodically; such forms are termed *polycarpic* plants. The most representative polycarpic plants are trees and shrubs, in which the shoots do not die down after flowering; in rhizomatous and bulbous plants, however, each shoot dies soon after flowering, much as in annuals, and new shoots arise by vegetative reproduction.

Probably in the majority of the perennials of temperate climates, the vegetative and reproductive periods, to some extent at least, alternate with one another, the flowering period being rather sharply defined, and often of short duration. Excellent cases of such alternating periods occur among plants with vernal flowers, as in the willows and poplars, and in such herbs as *Hepatica* and *Sanguinaria*, which bloom before vegetative activity begins. In such plants reproductive activity

merely appears to antedate vegetative activity, early flowering being possible only because of the food accumulated during the previous season; for that matter, the reproductive period in such plants begins in the spring or in the summer previous to flowering, and in some cases (as in the alder and hazel) the buds are fully formed before winter begins (fig. 541). In many plants the spring and summer are periods of vegetative activity (as in the goldenrods, asters, gentians, and witch-hazel), while the reproductive period falls in the late summer or in autumn. In some plants (as *Satureja* and *Lechea*) there are strongly marked vegetative periods in spring and in autumn, separated by the summer reproductive period. An unusually sharp contrast between vegetative and reproductive activity is afforded by the wild leek (*Allium tricoccum*) and by the meadow saffron (*Colchicum autumnale*), in which the leaves appear in spring and soon die down, while the flowers do not appear until summer or autumn.

There are many species in which the vegetative and reproductive periods are essentially coincident. In a few instances (as in *Dicentra* and *Claytonia*) the two periods not only are more or less coincident, but they are of short duration; in most cases, however, as in the chickweed (*Stellaria media*), the periods of vegetative and of reproductive activity are coincident and of long duration; such plants may be called *everbloomers*. As might be expected, everbloomers flourish particularly in uniform tropical climates. While in temperate climates each month or even each week from spring to autumn is characterized by the anthesis of particular species, in uniform tropical climates almost any species may bloom at almost any time, and a large number of species are true everbloomers, being in flower at all times. Even those species which are strictly periodic in temperate climates may be everbloomers in the tropics (as in the grape and the Virginia creeper). In many species of tropical everbloomers there is a suggestion of periodicity, since some branches bloom at one time and some at another; for example, in the grape one shoot on a given vine may be putting forth leaves and another flowers, while still another is bearing ripe fruit. In such species the phenomena exhibited by an individual branch are periodic, but taking the plant as a whole the phenomena may be termed *spasmodic*. The most representative everbloomers are plants with unbranched trunks, such as *Cocos* or *Carica*, for in them there is essential continuity in both vegetative and reproductive activity in a given shoot; new leaves are found at all times, as well as flowers and

fruits in all stages of development. In many tropical plants, on the other hand, flowering is of relatively rare occurrence, several years or even many years elapsing between periods of anthesis. A very remarkable case of this sort is afforded by a bamboo, *Dendrocalamus strictus*, which is said to flower regularly at thirty-year intervals. Some tropical plants and even some plants of high latitudes (as the duckweed) are almost never seen in blossom, their reproduction being essentially vegetative.

The relation of anthesis to meteorological factors. — While the occurrence and the duration of flowering periods often have been regarded as due to inherent causes, it always has been known in a general way that climatic factors may hasten or retard such periods and modify their length. If vernal plants bloom sooner than usual, the season is called "early," while delayed anthesis causes a season to be called "late." The observation of meteorological phenomena in connection with the periodic activities of plants, and particularly of temperature in relation to anthesis, is known as *phenology*. In a general way it is known that temperature, among other factors, bears an important relation to flowering, which is facilitated by high temperatures and retarded by low temperatures. Phenological observers, however, often have regarded temperature as of such controlling importance that they have prepared tables showing the total amount of heat necessary for flowering in the various species. Such tables are almost worthless, since they fail to include the many other factors involved, some of which, as soil moisture or atmospheric moisture, equal or surpass temperature in importance. Further, in preparing tables, temperatures below 0° C. commonly are ignored, although they are certainly of considerable significance in some plants (as in those of arctic regions), while the temperatures just above 0° C. may be without significance in other plants (as in palms).

The difficulties involved in discovering the factors that determine the inception of anthesis are best illustrated in those species which form flower buds early in the season previous to flowering. Some buds, as in the lilac and the white birch, begin to develop a year before they come into bloom, and in most vernal species the flower buds are in evidence by midsummer. The insufficiency of the phenological method in the case of such plants is most striking, since certain buds (as in the alder and the hazel) that withstand days and even weeks of warm weather in the autumn without blooming require but a few days

of warm weather in spring to induce anthesis.[1] Years ago it was shown that summer and autumn temperatures have little or no influence upon the flower buds of the cherry (*Prunus avium*), though the buds are evident as early as July; however, shoots taken into a hothouse in the middle of December bloomed in twenty-seven days, whereas those taken in the middle of January, in early March, and in early April, bloomed, respectively, in eighteen days, in twelve days, and in five days. In some comprehensive experiments with nearly three hundred species of woody plants, more than half of the twigs which were brought into a greenhouse in November started to grow within two weeks; the twigs of seventy species began to grow in February, and those of thirty-six species did not become active until March. These results make it very obvious that the influence of temperature or of other external factors upon anthesis depends entirely upon the condition of the buds at the inception of the experiment. While buds in February look much as they do in December, in reality they are different, one determinable change being that in winter there is a gradual increase of available food in the embryonic organs; probably this relative absence of available food is one of the chief reasons why autumnal buds open so tardily or remain closed, when they are exposed to favorable temperatures.

It is probable that buds undergo progressive changes other than those related to the food supply, though the nature of such changes is unknown. It has been shown that the development of buds can be greatly stimulated by various methods of treatment during the early part of the resting period. For example, the subjection of resting buds to anesthetics, to freezing temperatures, to warm water baths, or to various methods of chemical treatment, results in a material shortening of the rest period, provided the plants are brought subsequently into conditions suitable for bud development; as might be expected, this artificial hastening of development has proven to be of great commercial advantage in the " forcing " of bulbs, and of lilacs and other ornamental shrubs. The exact effect of these methods is imperfectly known although it has been shown that such treatments of dormant potato tubers have been effective in breaking their rest

[1] Occasionally vernal species flower in autumn (as in the violet, strawberry, and apple), particularly if favorable temperature and moisture conditions are long continued. The wonder is that such phenomena are relatively rare, especially since some buds seem to be fully formed by early autumn (as in the alder and the hazel).

period and that such treated tubers exhibited a decided increase in their sucrose content and a corresponding decrease in starch. It seems probable that similar chemical changes occur in the buds of the woody plants mentioned above.

Flowering periods in arid and in frigid climates. — In uniform tropical climates, the flowering of plants does not characterize any one season more than another, many species even being everbloomers. In most temperate climates, flowers appear at all seasons that are in any way favorable; estival flowering occurs chiefly at the expense of food accumulated in spring, but the earlier vernal flowers utilize the food accumulated during the previous vegetative period. In respect to anthesis, arid and frigid climates present certain features of marked contrast to temperate climates and to uniform tropical climates. In arid climates the inception of the rainy period is marked by vegetative activity, but this is checked at the beginning of the next dry period. Flowering, however, is to a large extent associated with the dry period; indeed, in many cases, anthesis is as definitely associated with the dry season as is vegetative activity with the rainy season. In the monsoon district of eastern Java, where the year is about equally divided into two periods, one of considerable rain and the other of drought, more than 60 per cent of the species bloom solely in the dry period, while only 8 per cent bloom solely in the wet period; the remaining 30 per cent are either everbloomers or forms which overlap the two periods.

In alpine and in arctic climates the flowering period is very short, often not lasting more than two or three months. Plants that bloom in the lowlands in April (as *Erythronium* and *Claytonia*) may not bloom until June in alpine meadows, because of the long-continued cold and the tardy melting of the snow at high altitudes. Strangely enough, however, the alpine season soon catches up with that of the lowlands, so that by July similar forms may be blooming at all altitudes, and in August the alpine season actually is ahead of that of the lowlands; for example, goldenrods and gentians commonly blossom sooner in the mountains than at lower altitudes. Similarly, spring is much later and autumn much earlier in high than in low latitudes; the farther grain grows from the equator, the shorter is its maturation period, barley, for example, ripening in ninety days in northern Norway, but requiring one hundred days in southern Sweden. In part this surprising phenomenon may be due to the fact that alpine and arctic species

are different from the lowland species, and therefore, perhaps, inherently characterized by shorter periods. That this is a minor matter in the explanation, however, is shown by the fact that some of the species are common to high and to low altitudes (as the yarrow and the harebell), but particularly by the fact that alpine plants grown in the lowlands, or lowland plants grown in alpine districts, behave in each case precisely like the indigenous plants. Obviously, also, the usual phenological assumption that low temperatures retard anthesis is the very reverse of the fact, for the heat sums are much greater in low than in high altitudes and latitudes.

It has been suggested that the greater intensity of alpine light and the greater duration of arctic light, respectively, account for the "hurrying up" of the seasons at high altitudes and high latitudes, enabling plants to make the food necessary for anthesis in a shorter time. The experiments about to be cited give another suggestion, namely, that those factors that are detrimental to vegetative activity and which, therefore, cause its early cessation, are at the same time favorable to reproductive activity. Among the factors in alpine habitats that tend to check optimum vegetative activity are low nocturnal temperatures, great temperature differences between day and night, high transpiration in proportion to absorption, and, perhaps, intense light.

The experimental determination of vegetative and of reproductive periods. — Adequate experimental study has shown that the length of the initial vegetative period (*i.e.* the period from germination to anthesis) and the length of the reproductive period are subject to wide modification through the operation of external factors, and it has been found possible also to extend the initial vegetative period indefinitely by the inhibition of reproduction. These experiments shed much light upon the phenomena cited in the preceding pages. Many interesting facts concerning reproductive periods have long been recognized, because of their important practical bearing. For example, crops like peas, tomatoes, and sweet corn may mature some days or even some weeks sooner on dry, well-lighted slopes than in rich, moist lowlands, so that the profit from the former is often much the greater; but in crops where the vegetative organs are marketed, the rich, moist habitat often is preferable, because of the greater luxuriance of the foliage. Comparable phenomena are exhibited by trees, *Pinus silvestris* maturing fruit in fifteen years if standing alone in dry soil, but requiring

thirty to forty years in a grove; similar differences are seen in the beech and in many other trees.

Early reproduction, which often is of great practical benefit, frequently is brought about by various mechanical means. *Picea excelsa*, which commonly flowers in thirty to forty years, may be induced to flower in four to ten years by transplanting, especially if the roots are injured. Orchard trees often fruit much better if some of the roots are removed. Girdling sometimes induces flowering in apple trees that otherwise exhibit only vegetative activity. Shoots of a young tree grafted on an old tree bloom much sooner than those that are left on the young tree.[1] Cuttings bloom long before seedlings, a matter of the highest economic importance. Of much interest is the fact that a cutting from an old plant blooms much sooner than one from a young plant, though the cuttings may be of equal size and similar aspect. This phenomenon is most strikingly displayed in leaf cuttings (as in *Begonia* or *Achimenes*), in which the young shoot flowers almost at once if the leaf is taken from a flowering plant, but only after a long time if taken from a young plant. This phenomenon has been explained by postulating the accumulation of *flower-forming substances* in plants approaching maturity, but this assumption needs explanation as much as do the facts which it attempts to explain. Furthermore, there are some cases, as in *Torenia*, where leaf cuttings flower at once almost regardless of the age of the part of the plant from which the cutting is taken. At any rate, the maturity of the flowering plant seems to be in some way transmitted to the propagule.

It has been proved conclusively that plants may be kept in a vegetative state indefinitely, and that the usual successive stages in a plant's life history are reversible. For example, when the ground ivy (*Nepeta hederacea*), which commonly has a reproductive period intercalated between the vegetative periods of spring and autumn, is grown in a greenhouse under uniform conditions of moderate temperature and considerable moisture, vegetative activity continues uninterruptedly. However, flowering may be induced at any time by transferring the plants to a dry, well-lighted situation. Similarly, by exposure to proper external conditions, "winter buds" have been induced in *Utricularia* at any season, hyacinths have been induced to

[1] For example, when a twig from an apple sapling is grafted on an old stock, it may fruit in a year or two instead of in ten or fifteen years, while a twig from an old stock grafted on a sapling does not fruit for many years.

flower twice without an intervening period of rest, and *Parietaria* has been kept in constant bloom. Annuals have been transformed into biennials or perennials by keeping them under constant conditions favorable to vegetative activity, and *Echium*, which usually is a biennial, has been known to grow in the tropics ten years without flowering

FIGS. 505, 506. — Variation in the flowering shoots of *Veronica chamaedrys:* 505, an ordinary flowering shoot with buds, flowers, and young fruits; 506, a similar shoot that was placed in moist air at the inception of anthesis; note the metamorphosis of the upper part into a leafy shoot. — From KLEBS.

When the annuals, *Poa annua* and *Senecio vulgaris*, are transferred to alpine habitats, the season is too short for fruit maturation and the plants become biennial. Many garden annuals may be transformed into biennials by removing the flower buds as they appear; in this manner the mignonette may be transformed even into a woody perennial. In monocarpic species life may be shortened by hastening reproduction, as well as lengthened by promoting vegetative activity; thus the castor bean, a tropical perennial, has been transformed into an annual in temperate climates, where the conditions facilitate early reproduction. The closeness with which death follows reproduction in monocarpic species is well illustrated in hemp, a dioecious annual; the staminate plants die immediately after anthesis, while the pistillate plants live until the fruit has matured, several weeks later. A number of plants which display vigorous vegetative reproduction (as the yam, the potato, and the sweet potato) rarely produce seeds, hence it has been suggested that seed production and vegetative production may be more or less mutually exclusive; however, there are many plants in which both kinds of reproduction are vigorous (as in the dahlia, the strawberry, and the willow).

The usual succession of events from the inception of vegetative activity to the maturation of fruit is so familiar that it has often been mistakenly referred to as normal, thereby implying that any change in the order of events is abnormal. It has been shown that the order is reversible at almost any point. In certain species of *Veronica*, for

example, if an inflorescence is cut off and allowed to strike root in a moist chamber the tip grows into a vegetative shoot (figs. 505, 506). The oldest buds develop into the usual flowers, while younger buds develop into cleistogamous flowers without prominent corollas; still younger buds develop only the calyx, and the very youngest lateral buds, as well as the terminal bud, develop vegetative shoots. If a flowering shoot of *Myriophyllum heterophyllum* is transferred from a pond to a covered aquarium, it becomes transformed into a vegetative shoot. *Ajuga reptans* has three phases, a rosette, a flowering shoot, and a stolon, and any of the three can be induced at any time by supplying the requisite external conditions. If the flowers of *Opuntia* are removed from the plant and placed in the soil, they soon strike root and give rise to vegetative shoots. Most striking of all, perhaps, are the reactions of the xerophyte, *Sempervivum*, which also has three phases, comparable to those of *Ajuga;* vegetative activity may be made to continue indefinitely, stolon formation may be eliminated, and phenomena unusual in nature (such as rosette formation at the stem apex, and the transformation of the inflorescence into a vegetative shoot) may be induced at will.

Reversibility of stages is not confined to the seed plants; if a fruiting shoot of *Selaginella lepidophylla* is cut off and placed in the soil of a moist hothouse, it becomes transformed into a vegetative shoot, even developing rhizophores. Reversibility can be induced also in animals, for if a polyp of the hydroid, *Campanularia*, is brought into contact with a solid body, it gradually becomes undifferentiated and finally develops into a stolon, whereas removal to the original habitat soon results in a transformation back to a polyp. It may be noted finally that reversibility is the usual thing in the pineapple, a vegetative shoot developing at the apex of the fruit.

The above experimental evidence compels the abandonment of the notion that only the usual succession of events in a plant in nature is to be considered normal. One thing alone is fixed, namely, that plants must at the outset have a period of vegetative activity, but whether this continues through life, or whether the reproductive period begins early or late or not at all, is a matter that is determined by external conditions, and one series of events is quite as normal as another. It is quite as normal for a bulrush to live in deep water and to vegetate indefinitely as to live in shallow water and to flower annually. Indeed it is permissible to regard anything that a plant ever does as normal, since in every case its particular reactions are due to its life conditions. Thus it is demonstrated that plants as a rule do not possess an inherent

rhythm, since external factors are the dominant determining causes of reproductive periods; if plants flower regularly, the requisite conditions may be supposed to recur regularly.

The exact analysis of the reproductive factors remains to be determined, though the data now available are sufficient to show that successive stages imply successive causes (*i.e.* changed conditions), while uniform phenomena imply uniform or unchanged conditions. Broadly speaking, the conditions commonly termed hydrophytic and mesophytic seem especially to favor the continuance of vegetative activity, while xerophytic conditions favor reproduction. Hence it is not unlikely that the amount of available water may be a dominant specific factor, especially as its presence in abundance is known to be a primary requisite for optimum vegetative development.

FIG. 507. — Cosmos plants about 60 days old; those at left receiving light for 6 hours daily are in bloom; those at right with 15 hours of light daily are larger and completely vegetative. — After WEAVER.

Photoperiodism. — Another important reproductive factor is light. Careful experiments on *Mimulus* show that light of high intensity favors flower production. In the giant cactus there is a ring of flowers about the stem and anthesis begins on the side toward the sun. Many plants, however, show a more direct response to the length of day, that is, to the daily relative duration of light and darkness, than to the intensity of the light. A large number of species are more or less responsive to the length of the daily light period, and this response has been termed *photoperiodism*. Most spring flowers, like the violet, hepatica, and anemone, flower at a season of the year when the light days are only ten hours long. Common blue violet flowers may be produced at any season of the year, however, by exposing the plants daily to ten hours only of sunlight. In a similar way some autumnal plants like the chrysanthemum and cosmos bloom only during the short days of the fall but may be brought into flower at any season of the year by being exposed to a short light day (fig. 507).

In contrast with these conditions many of the summer blooming plants, like clover and soy beans, flower only with long daily illumination. The rose-mallow, for example, does not flower unless exposed daily to more than twelve hours of light. Other plants are not so sensitive to *photoperiods* and, like the dandelion or buck-

wheat, flower with any daily illumination of six to eighteen hours. It would seem from recent investigations that three classes of plants may be distinguished on a photoperiod basis: short-day, long-day, and everblooming plants.

Photoperiods affect other activities of plants as well as their flowering season. Common garden vegetables may greatly vary in these responses. Thus an early radish, if exposed to a seven-hour-light day will continue to enlarge its bulbous root for many months, while with the same light exposure a carrot will scarcely thicken its root, but under a fourteen-hour day large thick carrots are developed. An apple seedling grows most vigorously with a ten-hour day, while a young box-elder will not thrive with less than fourteen hours of daily illumination. Different branches of the same plant will sometimes respond to different photoperiods. The common cosmos, a short-day plant, if made to develop two nearly equal branches and one branch be given ten and the other fifteen hours of light daily, will develop flowers and ripen seed on the short-day branch while the long-day branch will continue vegetative growth without flowering for an indefinite period. Cosmos plants under a short day will develop dwarfed plants that may flower within 60 days from seed, while under long-day illumination they continue growth indefinitely and may attain a height of 12 to 15 feet.

Experiments also seem to indicate that length of day has a decided influence on tuber formation. Certain Mexican plants (*Solanum demissum*, *S. acaule*, etc.) closely related to the cultivated potato, show a vigorous development of leaves and stems but produce no tubers under long-day conditions. When grown under a ten-hour photoperiod they show short stems, weak vegetative growth but develop an abundance of tubers.

These reactions obviously limit the geographical distribution of plants, for those that require a long day for flowering and seeding cannot maintain themselves in the tropics where the day remains at 12 hours for the entire year. The extreme types of short-day plants would also be excluded from the tropics unless they found themselves able to persist vegetatively. Length of day should therefore be taken into account in any exact study of factors affecting distribution and should be considered when artificially introducing plants to a new region. Only everblooming plants seem equally suited to the light conditions of both the tropical and temperate zones.

The influence of external factors upon sex determination. — The great majority of plants appear to be strictly monoclinous or diclinous, the latter being for the most part strictly monoecious or strictly dioecious. As previously noted, however, there are a number of species, which vary between monocliny and decliny or between monoecism and dioecism. It is particularly among such plants that experimentation has been carried on regarding sex determination. When maize (*Zea mays*) is grown under favorable vegetative conditions, the plants commonly are monoecious, but when it is grown in dry, sterile soil or is exposed to weak light, a small unbranched plant develops, which produces only a staminate inflorescence. Even under ordinary growth

conditions, the staminate flowers originate first, and it has been suggested that the pistillate flowers come later when the nutritive conditions are more favorable. When the nutritive conditions are very favorable, or when the primordia are parasitized by smut, pistillate flowers may be induced in staminate inflorescences. Most of the catkin-bearing trees resemble maize in that the primordia of the staminate flowers develop earlier than do the primordia of the pistillate flowers. In *Picea* and in some other conifers, pistillate flowers occur only on the more vigorous and better nourished shoots, while the staminate flowers occur on weaker shoots. When *Satureja hortensis* is grown in rich soil and is well illuminated, 79 per cent of the flowers are monoclinous, the remainder being pistillate; in poor soil and under poor illumination only 13 per cent are monoclinous, the remaining 87 per cent being pistillate only.

It is a general belief that in dioecious plants xerophytic conditions (or conditions of food impoverishment) facilitate the development of staminate plants. The experiments cited above favor this view, but there certainly are other factors concerned. It has been claimed, for example, that large seeds are likely to develop into pistillate plants and small seeds into staminate plants. The hemp (*Cannabis sativa*), which is a representative dioecious plant, may grow in rich alluvial soil, where it displays great vigor, or in dry waste soil, where plants are weak and impoverished, but in all cases both staminate and pistillate plants are found if there is a large number of individuals. When grown in the greenhouse in winter under poor light conditions, hemp displays many sexual irregularities, pistillate plants showing reversal to maleness, and staminate plants reversal to femaleness. The common Indian turnip (*Arisaema triphyllum*) is a dioecious plant with a considerable number of intermediate individuals. Grown under unfavorable conditions, purely pistillate plants have been changed into purely staminate, and then by improving the conditions a reversal has taken place and the staminate plants have become again pistillate.

Among dioecious perennials (such as the box-elder, poplars, and willows) the same individual usually bears the same kind of gametophytes, regardless of external conditions, so that two individuals which appear alike when not in flower are really different, the one transmitting male attributes and the other female attributes. There are on record, however, some noteworthy cases of change of sex on the part of indi-

vidual plants. In some of these the sex has been changed by wounding (traumatism). The primordia of pistillate inflorescences of maize have been subjected to torsion and thereby changed to staminate inflorescences; also staminate inflorescences have been changed to pistillate. By varying the photoperiod it has been found possible to produce, at will, pistillate or staminate inflorescences in maize. By injuring the terminal bud of a staminate plant of *Carica papaya*, the plant has been stimulated to produce pistillate flowers which have matured into fruits. *Pulicaria dysenterica* commonly has monoclinous flowers, but when the subterranean organs are infested by *Baris analis*, an insect parasite, the species becomes dioecious.

Notwithstanding the experiments cited above it is now generally believed that the sex of an individual is not due to the external conditions to which the individual itself may be subjected, but that sex is determined much earlier than had been supposed. In seed plants sex differentiations are always present in the gametophytes, while it would seem that the sporophytes may be of any grade from male through hermaphrodite to female. The sex of the gametophyte is determined at least as early as at the reduction division. In the liverwort, *Sphaerocarpus*, sex is determined at the time of spore formation, since two spores of each tetrad give rise to male plants and two spores to female plants. In heterosporous pteridophytes and in seed plants the sex of the gametophyte seems to be determined long before spore formation, since it depends upon the kind of sporangium that is produced by the preceding sporophyte.

On the other hand, in homosporous pteridophytes and in monoecious mosses, sex determination appears to come much later than spore formation, and to depend in part, at least, upon the conditions to which the gametophyte is exposed. A remarkable situation has been disclosed in the dioecious mosses, in which sex is determined at spore formation, half of the spores giving rise to male plants and half to female plants, as in the liverwort, *Sphaerocarpus*. Pieces of the sporophyte may give rise vegetatively to gametophytes, and such gametophytes are bisexual, whereas gametophytes that develop from spores are unisexual. Hence it appears that the supposedly nonsexual sporophyte is in reality bisexual.

Variations in flower color. — The most variable character of flowers is that of color. Many cases of color variation in flowers of the same species clearly are due to external factors, particularly in those flowers

in which colors are due to anthocyanin;[1] such variations may be quantitative, involving differences in intensity only, or they may be qualitative, involving differences in wave length. Light seems to be the most important factor determining variations in color intensity. It was discovered long ago that when bulbs (as in the tulip or hyacinth) are grown in the dark, they develop colored flowers much as in the light, though the color intensity is less, sometimes being much less, as in blue hyacinths. Coloration takes place in the dark in some non-bulbous plants, such as *Lychnis*, *Hydrangea*, and *Papaver*. In striking contrast to bulbous plants are *Antirrhinum* and *Prunella*, where the food necessary for anthesis does not accumulate during the previous season, but is manufactured just before the period of floral development. In such plants the flowers do not become fully colored when the entire plant is grown in the dark, as in the tulip, although they become colored if the vegetative shoots are grown in the light and the floral shoots in the dark. Even tulip flowers do not become colored in the dark unless the previous leaf generation is exposed to sunlight. Thus the influence of light upon color intensity appears to be in part direct, as is indicated by the deep shades of hyacinth flowers that are grown in the sunlight and by the high intensity of color of alpine flowers. However, to an equal or greater extent the light influence is indirect, as is well shown by those flowers that become colored only when the leaves are in the light. The color in this case and in the dark cultures of bulbous plants seems to be associated with a rich food supply, a fact which is quite in harmony with the sugar theory of anthocyanin formation. Probably in the majority of flowers, direct exposure to sunlight is required to produce full coloration, although a certain amount of pigmentation occurs in darkness. Yellow colors are much less weakened by darkness than are the anthocyanin colors. Heat as well as light affects coloration, the intensity often being heightened at low temperatures.

Variations in the quality or kind of color are much less understood than are variations in color intensity, though it is known that the cell sap of red anthocyanin flowers is more acid than is the cell sap of blue anthocyanin flowers; hence it is to be supposed that factors which

[1] However, there are some striking cases of color variation in flowers whose color is due to chromoplasts, as in *Tropaeolum* and in *Castilleja coccinea;* the latter is more likely to have scarlet flowers in rich soil, where the plants are vigorous, and lemon-yellow flowers in peaty soil, where the plants are impoverished.

cause variations in the acidity of the cell sap cause variations in color also. The flowers of *Hydrangea hortensis*, which usually are red, become blue when the plants are grown in soil containing a considerable amount of the sulphates or of other salts of aluminum and potassium. Aluminum salts frequently change lilac-colored flowers to blue, whereas potassium salts may change them to green. Acids, on the other hand, frequently change flower colors to red. White roses have been changed to red by adding potassium salts to the soil. Heat affects the quality as well as the intensity of flower color, low temperatures, for example, sometimes causing white geraniums to become red or rose geraniums to become carmine. The flowers of harebells and morning-glories also vary with the temperature in respect to color quality (see also p. 360).

There are some instances where color variation may not be due to external factors. *Hepatica* plants, in apparently similar conditions, exhibit various colors from pink to blue. Perhaps the most probable instance of " inherent " color characters is in the albinos, which seem to have white (*i.e.* unpigmented) flowers in any habitat; such albinos are known in many plants (as in *Lupinus* and *Sisyrinchium*), and in some cases there are comparable variegated flowers (as in *Viola cucullata*). Albinos commonly are regarded as sports or mutants, but the possibility of external determining factors even here is suggested by the reported pigmentation of *Trillium* albinos that have been transplanted to a new habitat.

Variations in the size and number of floral organs. — When plants are grown in very poor nutritive conditions, the number of flowers on each individual is much reduced, and sometimes (as in the poppy) the size of the flower also is reduced. Weakened illumination may cause a decrease in flower size, particularly in the size of the corolla (as in *Mimulus*); by contrast it is to be noted that in xerophytic alpine habitats, in spite of the marked reduction of other organs, there is no marked reduction in flower size, probably because of the intense illumination (figs. 358, 359). In poorly nourished specimens of *Agrimonia*, the stamen number may be reduced from about twenty to five. When the poppy is grown in dense cultures, the number may be reduced from thirty or forty to six; this result is most significant, since in this group the large number of stamens is an important taxonomic character. Equally significant is the carpel variation in the poppy; in well-nourished individuals there may be one hundred and fifty carpels, but in poorly nourished individuals the number may be reduced to four. In *Chrysanthemum* and in some other composites, the number of ray flowers varies with the

nutrition, well-nourished plants having the largest number of such flowers. A remarkable situation is presented in *Sempervivum*, in which there have been produced all gradations between flowers and vegetative shoots; some flowers lack corollas, others lack stamens and pistils, and even the calyx, which usually is the most certain of development of floral organs, sometimes is absent, in which event the bracts alone represent the floral organs. In this genus also it is possible to induce the transformation of stamen primordia into carpels, or of carpel primordia into stamens. Similar results have been obtained in *Veronica* (p. 408).

Variations in flower form. — Perhaps the most significant of all the variations in reproductive structures are those involving changes in form, since they have to do with the very fundamentals of classification, and therefore are likely to shed important light upon the processes of evolution. It was shown long ago that various zygomorphic flowers owe to gravity their peculiar shape, since they become actinomorphic when its influence is equalized. In *Mimulus*, zygomorphy is reduced in weak illumination. Floral symmetry has been modified also by cutting conductive strands that lead to the flowers and by otherwise changing the nutritive conditions. Of particular interest are the experimental data on cleistogamy, which involves marked change of form and structure, especially in the corolla. In *Stellaria*, light is required for the opening of the flowers, and in *Linaria*, flowers that usually are chasmogamous in weak light are cleistogamous. In *Lamium* the vernal and autumnal but not the estival flowers are cleistogamous. In *Impatiens noli-tangere* the first flowers usually are cleistogamous and spurless, while the later ones are chasmogamous and spurred; but if such a plant is transferred to sterile sandy soil, only cleistogamous flowers are produced, indicating that poor nutrition favors cleistogamy. Chasmogamous flowers may be produced by *Stellaria* even in weak light, if the plants are supplied with glucose. Parasites may induce cleistogamy; mildewed plants of *Impatiens* produce only closed flowers, and *Biscutella* produces such flowers, when the plants are attacked by cecidomyid insects. In *Viola mirabilis* the primordia of chasmogamous flowers develop into closed flowers in extreme conditions, as in dry, sterile soil and in a warm, humid greenhouse, and in *V. odorata* the primordia of the cleistogamous flowers develop into showy open flowers in dryish, sunny habitats.

A most interesting floral modification is that seen in the so-called *double flowers* (figs. 508, 509). Where the phenomenon is one of the replacement of other floral organs (especially stamens and pistils) by petals, it may be denominated *petalody* or *petalization*.[1] There are varying degrees of petalody; for example, the buttercups, which commonly have five petals, may have the number doubled or otherwise increased even to complete petalization. In the white water lily (*Castalia*), in which there are many petals disposed in several rows, the inner members become smaller and narrower, and show all transitions to stamens. Passing outward from the center, the stamen filaments become broader and more petaloid, while the anthers gradually become effaced, suggesting the possible origin of petals from stamens or of stamens from petals; the first theory is the more reasonable, but there is no valid evidence for either. The exact cause of petalization is unknown, but in many cases it appears to be inherent, double flowers usually being regarded as sports or mutants, since they often may be reproduced by seed as well as by cuttings.[2] In other cases, petaliza-

FIGS. 508, 509. — Flowers of *Narcissus*, illustrating petalody: 508, an ordinary single flower with a six-parted perianth (*p*) and a crown or corona (*c*); 509, a double flower, in which there is a considerable increase of the petaloid parts at the expense of the stamens and carpels.

[1] In the composites, however, doubling is due to the replacement not of stamens by petals, but of disk flowers by ligulate flowers (as in double sunflowers and chrysanthemums), so that one should speak of double heads rather than of double flowers.

[2] Obviously, completely petalized flowers can be reproduced only by cuttings. In the double petunia, which usually is propagated from seed, seeds are saved from flowers that are almost double, and only 20 to 30 per cent of the progeny have double flowers. In the composites complete doubling does not necessarily prevent seed production, double asters, daisies, and sunflowers being raised regularly from seed.

tion clearly is due to external factors, notably in a number of species in which plants whose roots are infested with certain parasitic fungi (as *Heterodera radicicola*) develop double flowers. *Saponaria* sometimes has double flowers when the roots are infested with *Fusarium*. In the tulip, petalody is facilitated by good nutrition, especially if there is an abundance of nitrogenous substances in the soil. In some cases parasites cause not only ordinary doubling, but also the development of green foliage leaves in place of floral organs, the phenomenon being known as *sepalody* or *greening*. In parasitized individuals of *Helianthus strumosus*, greening is a common phenomenon, and not infrequently green foliage leaves are intermingled with ligulate flowers in place of the usual disk flowers.

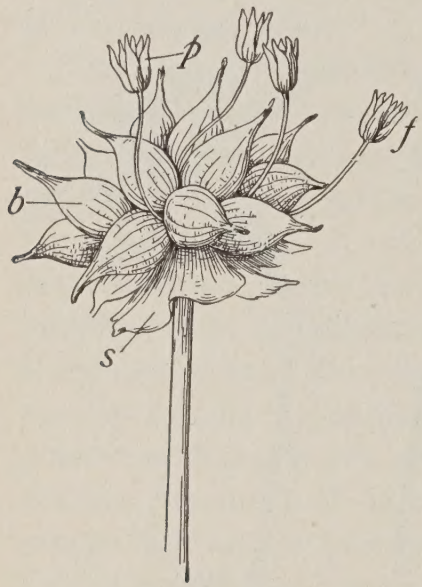


FIG. 510. — An umbel of the wild garlic (*Allium canadense*), in which there are only a few flowers (*f*), their place being taken largely by bulbils (*b*), which readily propagate the species vegetatively; *p*, perianth segments; *s*, spathe.

One of the most remarkable of all reproductive variations is that in which flowers are replaced by *bulbils*, as in the wild garlic (*Allium canadense*, fig. 510), in whose umbels some primordia develop into flowers and others into bulbils. Sometimes most or even all of the primordia develop into flowers, and again nearly all of the primordia may develop into bulbils. Usually the bulbils germinate while still attached to the inflorescence, but they are readily detachable, and they continue growing if they fall into favorable situations. Similar bulbils occur somewhat regularly in certain alpine plants, such as *Polygonum viviparum*, *Poa alpina*, and *Saxifraga*. The cause of such bulbil formation is not clearly known, though in the grasses, seeds rather than bulbils appear to be produced when the plants are grown in dry conditions or in media that are poor in nitrogen. That bulbil formation in alpine plants probably is a reaction to alpine conditions is indicated by the fact that *Gagea* plants taken from lowland to alpine habitats produce bulbils rather than flowers in the first season of culture. In the onion this habit affords the plant the apparent advantage of an additional method of reproduction, supplementing reproduction by

seeds and by subterranean bulbs; in alpine plants bulbil formation may be more certain than seed maturation, owing to the shortness of the season.

The factors determining the development and form of the organs of vegetative reproduction have been sufficiently considered elsewhere. It may be noted merely that in specialized organs, such as tubers and bulbs, xerophytic conditions may favor development, much as in other kinds of reproductive organs. For ordinary vegetative reproduction, however, particularly where it is indistinguishable from the usual phenomena of growth, mesophytic or hydrophytic conditions are more favorable.

In conclusion, it is now clear that external factors play an important part in determining the variation of reproductive organs. How great this part may be, and what the precise external factors are, remain as yet in large part unknown. It cannot suffice to explain phenomena by such terms as " bad nutrition " or " xerophytic conditions," though to attribute them to such a cause-complex is vastly more satisfactory than to refer them to inherent or internal causes.

Hybridization. — When related forms, not of the same species or variety, are crossed, the process is known as *hybridization* and the progeny are known as *hybrids*. Plants differ widely as to their hybridizing power. Most cultivated races derived from a common specific ancestor hybridize readily; some closely related species also hybridize readily, as among the oaks and willow, while others do not, as the apple and the pear, or the tomato and the nightshade. Occasionally different genera hybridize with each other, as *Brassica* and *Raphanus*. The notion is rather prevalent that hybrids generally are sterile, but among plants comparatively few sterile hybrids are known, one of the most probable cases being that of the horse radish (*Cochlearia armoracia*). Probably the greatest tendency to sterility is among forms that are very closely related (as in the case of close-pollination) or in forms whose relationship is so remote that crossing is difficult of accomplishment. Frequently hybrids are intermediate between their parents, showing a blending of characters, but there may be all degrees of likeness to one parent or the other. Sometimes, however, entirely new characters are introduced. In recent years the study of hybrids has assumed unusual proportions through the rediscovery of " Mendel's law."

Bud variation. — Occasionally plants have been known to give rise to a branch that is different from the others, and whose progeny resem-

bles this branch rather than the rest of the plant. Vegetative mutations of this sort are known as bud variations. Among bud variations are: witches' brooms on spruce and other trees, whose seeds give rise to bushy shrubs rather than to ordinary trees; white shoots on bean plants, whose progeny also is white; and yellow-fruited branches on red tomato plants. The nectarine is thought to have arisen as a bud variation of the peach. Most cases of bud variation seem to involve the loss of a character (such as greenness in the bean, or hairiness in the nectarine fruit), or the change of color (as in the tomato). The factors involved in bud variation are quite unknown.

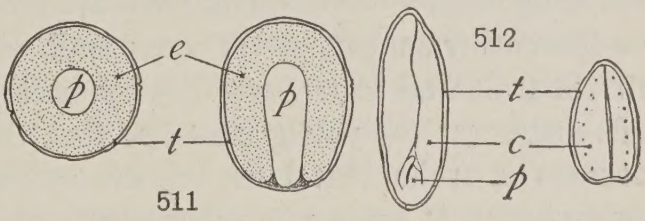
4. FRUITS AND SEEDS

The nature and rôle of fruits. — In the seed plants the fusion of the sperm and the egg is followed usually by certain changes in the floral organs, the most conspicuous of which is the enlargement of the ovary, as the ovules develop into seeds. Of the other floral organs, the corolla and the stamens soon disappear, but the calyx and the receptacle often enlarge with the ovary. The structure thus arising from the flower, through the enlargement of the ovary with or without the modification of other organs, is called the *fruit*, and obviously its chief rôle is the protection of the developing seeds. Most young fruits contain sufficient chlorophyll to make them conspicuously green, and they doubtless manufacture much of the food utilized in their development. Sometimes, as in the elm, green fruits are prominent before the leaves appear, or, as in *Cakile*, after the leaves have gone; in such cases the food-making rôle would seem particularly significant. At maturation the fruit by reason of its edibility and showiness often is a means of attracting seed-dispersing animals, and in other ways it is connected with the process of dissemination.

General characteristics of seeds. — *Morphology.* — The *seed*, which is an enlarged and matured ovule, is one of the most complex organs found in plants. The ovule, which is a sporophytic organ, serves as a domicile for the female gametophyte, and afterwards for the new sporophyte that develops from the fusion of the sperm and the egg. This structure, which thus is made up of elements from three generations, grows to a certain size, varying with the species, whereupon the integument develops into the *seed coat* or *testa*, and the growth of the sporophyte within is checked. Henceforth the structure may be called a seed rather than an ovule, so that a seed may be defined as

a young sporophyte in a state of arrested development, enclosed within a modified ovule integument, the testa; in addition, the gametophytic generation may or may not be represented by the endosperm.

Developmental features. — The ovules commonly arise on the margins of the carpels, to which they are attached by a stalk, the *funiculus*. The central mass of tissue, the *nucellus*, usually is enclosed by one or two *integuments* arising from the basal region (*chalaza*) just above the funiculus; the integuments do not close tightly about the nucellus, but leave a slender canal, the *micropyle*, through which the pollen tube usually makes its way. The ovules may be erect on the funiculus (*orthotropous*), partially pendent (*campylotropous*), or more commonly completely pendent (*anatropous*); in the last case the close application of the funiculus to the integument causes a suture, the *raphe*.[1] The young sporophyte or embryo at first grows vigorously, usually becoming differentiated at seed maturity into the embryo root (*radicle*), the embryo stem (*hypocotyl*), one, two, or more seed-leaves (*cotyledons*), and the embryo shoot (*plumule*).[2] The seed also contains foods that are utilized by the young sporophyte during its second phase of activity, commonly called *germination*.[3] These foods may accumulate within the cotyledons (as in peas and beans, fig. 512), which in that event occupy most of the space within the testa, or they may accumulate in a tissue surrounding the cotyledons (as in most monocotyls, fig. 511), this tissue being called *endosperm* if arising within the embryo sac, and *perisperm* if arising from the nucellus. Most seeds mature in the season of anthesis. Some plants with autumnal flowers, such as *Hamamelis* and *Colchicum*, mature seeds the following season, and in some plants with vernal flowers, such as the pines and certain oaks, maturation comes in the second season.



FIGS. 511, 512. — 511, cross and longitudinal sections of a seed of *Canna*, showing the seed coat or testa (*t*), the perisperm (*e*), and the embryo (*p*); 512, longitudinal and cross sections of a bean (*Phaseolus*), showing the seed coat or testa (*t*), the cotyledons (*c*), and the plumule (*p*).

[1] Most of these terms apply also to seeds.

[2] In the orchids and in some parasites the embryo remains undifferentiated.

[3] Little or no food is found in minute seeds, as in those of the orchids.

The rôle of seeds. — Primarily seeds are disseminules, and many of their chief structural features are associated with dispersal. Of almost equal importance in many plants, especially in annuals and biennials, is their protective rôle, since in no other form is the seed plant so immune to danger as in the seed. Though they are often so regarded, seeds are in no sense reproductive organs. The reproduction of which the seed is the result, takes place previously within the flower, while the seed represents in a state of arrested development the protected offspring of that reproduction. Thus the unique feature of the seed plants is the separation of reproduction from protection and dispersal; post-reproductive disseminules, the seeds, take the place of reproductive disseminules, the asexual spores.

The protective structures and relations of seeds. — *The protection of developing seeds.* — Developing seeds are protected from transpiration and from other dangers by the ovary wall, which thickens and hardens into the fruit wall or *pericarp*. It has been thought that grazing animals might eat the young fruits, so that the sourness, bitterness, or hardness of fruits that later become edible have been regarded as advantageous in protecting them from such dangers. In some cases, as in the jimson weed (*Datura*), the chestnut, and certain gooseberries (as *Ribes cynosbati*), the fruits are spinescent.

The prickly pear (*Opuntia*) is especially interesting from this viewpoint, since the unpleasant bristles of the young fruits fall off as the fruit ripens, from which it has been inferred that the young fruit is protected from the fruit-eating animals which later scatter the ripe seeds. Such views are misleading in their implications, since most young fruits are not especially attractive to animals. Their unpalatability is a sign of immaturity rather than of protection.

The protective structures of mature seeds. — Seeds as a class are the most xerophytic of plant structures, since not alone in xerophytes, but also in mesophytes and even in hydrophytes, they generally are covered with hard and impermeable coats. So universal is the xerophytism of the seed that usually it is impossible to determine from its structure the habitat in which it grew. This xerophytism consists in three features: the thick and impermeable coat, the compactness of the tissues within the testa, and the small amount of water. The *testa*, or *seed coat*, commonly is single, being derived from the ovule integument (from the outer integument, in case there are two) through thickening, hardening, and other modification. In some seeds there is a second coat within the testa, and in others there is a structure outside the

testa, which is known as an *aril* (*e.g.* in the water lily). The testa at maturity usually is hard and bony, being composed of several or more layers of cells with greatly thickened walls; in the hickory nut it is made up of a number of layers of sclereids. Sometimes the testa is so hard that it is difficult to cut it with a knife, as in *Gymnocladus*. In most one-seeded fruits, such as the grains of cereals (fig. 518) and the achenes of the composites, the fruit wall or pericarp remains closed about the seed at detachment, and often is the chief protective layer, especially where it is hard and bony (as in *Lithospermum*). In some instances seeds are essentially without a protective outer layer; this is the case particularly in the Amaryllidaceæ, where the outer integument or the endosperm may become fleshy and green (as in *Hymenocallis* and *Crinum*).

The advantages of seed protection. — The chief dangers which beset seeds are premature germination, loss of viability, and destruction by herbivorous animals. Adequate protection is especially important in monocarpic species, above all in annuals, since the maintenance of the species depends absolutely upon the viability of its seeds. For months at a time annuals may be non-existent over vast tracts of country except in the form of seeds. While most trees, as the pines, spread only through the agency of seeds, the situation is different, since the same individual produces seeds a number of times. The adequacy of seed protection is well illustrated by the abundant annual recurrence of such weeds as the ragweeds, pigweeds, purslane, and Russian thistle.

Seed protection in relations to animals. — Many seeds are used as food by herbivorous animals. Often, as in the nuts that are eaten by squirrels and in the many small seeds that are eaten by birds, the protective coats are insufficient to give adequate protection, the survival of the species depending upon those seeds that chance not to be eaten. The likelihood of such survival is not so slight as it might seem, since most species produce many more seeds than would commonly be eaten, and many seeds fall to the ground and become hidden by leaves. The seeds of edible fruits might be thought to be in especial danger, but in most cases they pass through the digestive tracts unharmed. The smooth and slippery surfaces and the pointed ends of most such seeds make it probable that they will be swallowed whole rather than masticated, and the thick and hard testa prevents the destructive action of digestive juices upon the living contents. Sometimes the seeds, as in

the grape, are enclosed by a mucilaginous pulp that is likely to be swallowed whole, and sometimes they are protected by special structures, such as the cartilaginous layers within the apple.

The vitality of seeds. — The amount of protection exhibited by seeds is shown in no other respect so well as by their remarkable longevity. While some seeds (as in the willow and the cacao) die unless they germinate almost immediately, most seeds retain their viability for several months or even years, and a few may remain alive for many years.

There is a popular belief in the possession of extreme longevity by certain seeds. For example, it often is asserted that the reason for the development of a totally new kind of vegetation when a forest is cleared is that seeds which have lain dormant for years or even for centuries then for the first time have a chance to germinate; a much simpler explanation, however, is found in the ease of seed dissemination. Many people have believed that wheat buried many centuries ago with the Egyptian mummies has germinated in recent times when properly planted. While stories of this character are without foundation, nevertheless it is true that under proper conditions certain seeds may remain alive for many years. Among the longest-lived seeds are those of the legume family. In experiments made with dried seeds of considerable age (none under 25 years old), involving over 500 species belonging to 30 families, those of 23 species distributed among 4 families proved viable, 18 of these being among the legumes; in these experiments the oldest viable seeds had an age of 87 years. Other experiments indicate the maximum retention of viability by legume seeds to be 150 to 250 years. Other long-lived seeds are those of the lotus and other water lilies, the mallows, and some of the mints.

In the phenomena of longevity there are three features of special interest: the status of the living cells during this long period, the features of the seed that cause the retardation of death, and the nature of the factors that ultimately cause death. There have been two theories concerning the status of the living cells, namely, that they manifest very slight respiratory activity, and that they are in a state of suspended animation.

It is not possible at present to determine which theory of cell life is the more valid, but some experiments seem to give strong support to the theory of suspended animation. There is no adequate evidence of respiratory gas exchanges nor of any other metabolic activity in dry seeds; the very small gas exchanges that have been

noticed are quite as characteristic of dead seeds as of living seeds, and in the latter they are fully as prominent in the dead testa as in the embryo. Furthermore, the theory of suspended animation best accounts for the wonderful resistance of seeds to extreme temperatures; indeed, seeds can endure a temperature so low that activity of any kind under such conditions seems quite impossible. The likelihood that activities may take place in seeds has been suggested from the fact that recently matured seeds of certain species germinate poorly, if at all, while, without any obvious structural change or physiological activity, they germinate readily after a lapse of some months. However, this theory has become less tenable in view of the discovery that differences in the germinability of seeds are due chiefly to changes in the permeability of the dead seed coat. In any case the life processes of seeds, if present, are intracellular and anaerobic and are exceedingly minute in amount.

It is practically certain that the chief feature of seeds which retards premature germination and facilitates longevity is the impermeability of the enveloping coat, especially of the testa. In many instances the seed coats of desiccated seeds have been found to be nearly impermeable to water and to gases; the most impermeable of such envelopes are those of legume seeds, which, as has been noted, are about the longest-lived of all. The compact structure and the low water content of seeds are unfavorable to activity, and hence facilitate longevity. Certain short-lived seeds live longer in the soil than when dried, possibly because, unlike most seeds, they are unable to withstand prolonged desiccation.

It is not unlikely that in some cases longevity is due to much less obvious features than to seed coats. Seeds similar in structure and with envelopes equally impermeable vary widely in longevity. Still more striking in this respect are the minute asexual spores of the seedless plants. While the spores of *Equisetum* die if they fail to germinate almost immediately, moss spores that have lain dry in a herbarium for fifty years have been known to retain their viability; it seems improbable that such differences can be accounted for by differences in the spore coat, which is not noticeably dissimilar in the two cases. In the liverworts, however, it has been observed that the spores of xerophytic species may withstand desiccation for two years, whereas the thin-walled, green spores of semi-hydrophytic species lose their vitality very quickly.

The causes of the death of seeds are in part known and in part open to question. While water is necessary for the initiation of germination, it often is absorbed by seeds under conditions that are unfavorable for the continuance of the germinative processes. This is the case with many seeds which fall into the water, or which are subjected to low temperatures or to desiccation, immediately after the absorption of

water has begun. Such seeds soon decay, or at any rate lose their vitality. Submergence in water for a month results in the death of the seeds of many land plants, such as rye, oats, and maize. However, the seeds of many water plants (such as *Alisma* and *Sagittaria*) can withstand submergence for some years, probably because of the extreme resistance offered by the seed coats to the penetration of water. Even when seeds are kept in ordinary rooms, the changes in atmospheric humidity probably are sufficient to reduce longevity seriously, because of the hygroscopic properties of the integuments. Most seeds die within three months if they are continuously exposed to saturated air, the longevity increasing somewhat regularly as the percentage of humidity is reduced. Parsnip seeds die within two months at a humidity of 70 per cent, although they may be kept alive for three years when desiccated and placed in a vacuum. Apparently, then, the exemption of seeds from conditions that tend to incite water absorption, respiration, or activity of any kind is a necessity for longevity. It is probably for this reason that most seeds retain their vitality best when they are stored where conditions are uniformly cool and dry. Experiments show that certain seeds retain their longevity for a very long time when they are buried in the soil, though not so long as in dry storage. For example, seeds of mustard, dock, and purslane have been known to retain their vitality for twenty-five years, when buried at a depth of fifty centimeters.[1] It has been shown also that deep burial insures greater longevity than does shallow burial. Under such conditions, longevity would seem to depend largely upon the resistance of the seed coats to water. If the seeds are deeply buried, the conditions are relatively favorable for longevity, because of the uniformly low temperature and because of comparative freedom from exposure to air and to alternations of wetness and dryness in the soil.

While the amount of water in seeds is small, a portion of this amount is essential to life. Hence, it is probable that any seed would die if it were exposed to evaporation for a sufficient length of time, but the time may vary with the species from a few hours or days to hundreds of years. If continued respiration takes place in dry seeds, however slowly, it is obvious that death must sooner or later ensue. Conditions which are fatal to most other plant organs often have no deleterious influence upon seeds. For instance, dry seeds can be kept for some

[1] Seeds of the Indian lotus, *Nelumbo nucifera*, buried in damp soil, have retained their vitality for 250 years.

time without injury at a temperature of −210° C., even if the testa is perforated, and a long sojourn in a vacuum or in an atmosphere of carbon dioxide or nitrogen is not injurious. Extremely high temperatures also may be withstood without harm, but with them there is a recognizable limit, as is not the case with low temperatures. Most desiccated seeds can withstand for one or two hours a temperature of 100° C., and alfalfa seeds can withstand a short exposure to a temperature of 120° C., even when placed in water. Perhaps the severest test yet made has been with the seeds of alfalfa, mustard, and wheat, whose coats had been perforated and thus made permeable; these seeds germinated after having been subjected to desiccation for six months, and then placed in a vacuum for a year, and finally subjected for three weeks to a temperature of −190° C., and for three days to a temperature of −250° C. It may well be wondered why seeds should ever die if they can withstand such severe conditions. The seeds which have been reported to have retained their vitality for more than two centuries were subjected during this time to constant changes of humidity and temperature. It is impossible to conjecture how long they might have lived, had they been stored under conditions of uniform desiccation and refrigeration.

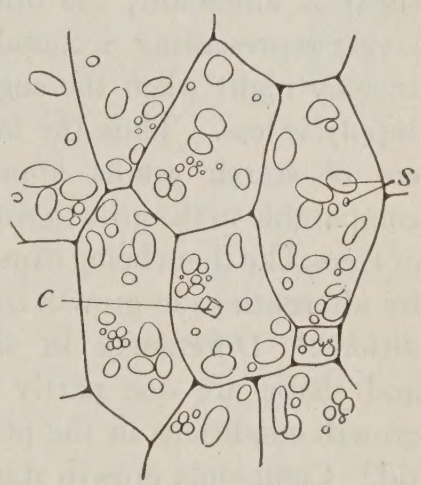


FIG. 513. — Cortical cells of a potato tuber (*Solanum tuberosum*), showing starch grains (*s*) of different sizes, and also a protein crystal (*c*); highly magnified.

Seeds as organs of food accumulation. — *Introductory statement.* — It has been seen elsewhere that foods accumulate in various organs, particularly in stems and in roots, but it is in seeds that food accumulation is most conspicuous, so that the chief discussion of plant foods has been reserved for this place. Seeds are filled with food more generally than is any other plant organ, and the kinds of foods reach here their greatest diversity in composition, form, and distribution. The foods in seeds and in other organs may conveniently be divided into those without nitrogen (such as the carbohydrates) and those containing nitrogen (notably the proteins).

Starch. — *Starch* probably is more generally accumulated in seeds and in other plant organs than is any other kind of food, being particu-

larly well known in the grains, in peas and beans, and in potato tubers. Starch grains differ widely in size, in shape, and in structure, these differences serving often to characterize particular species, genera, or families (figs. 513, 518). As previously noted, starch grains are produced through the activity of plastids; in seeds the plastids concerned are the colorless leucoplasts, the sugar that enters the developing seeds being transformed by them into starch. As the starch accumulates in the plastid, the peripheral portion of the latter expands until finally the protoplasm consists merely of a thin film enveloping the starch grain.[1]

FIG. 514. — A starch grain from the cortex of a potato tuber (*Solanum tuberosum*), showing the eccentric development of the rings of growth; very highly magnified.

The most obvious structural features of starch grains are their lines of stratification, which are due to alternating layers of different density (fig. 514). In the large grains of *Pellionia* and probably elsewhere the dense layers have been thought to represent accumulation by day when the sugar is abundant, the other layers representing accumulation by night when the sugar supply is less. Thus the layers of starch grains appear comparable to the growth rings of trees, like them being caused by alternations in growth conditions.[2] Differences in size and shape are due partly to growth conditions in the plastid. Commonly growth starts in the center (as in peas and beans), and the rings are parallel to the plastid periphery, the resulting grain being a symmetrical spheroid or ellipsoid. Sometimes growth be-

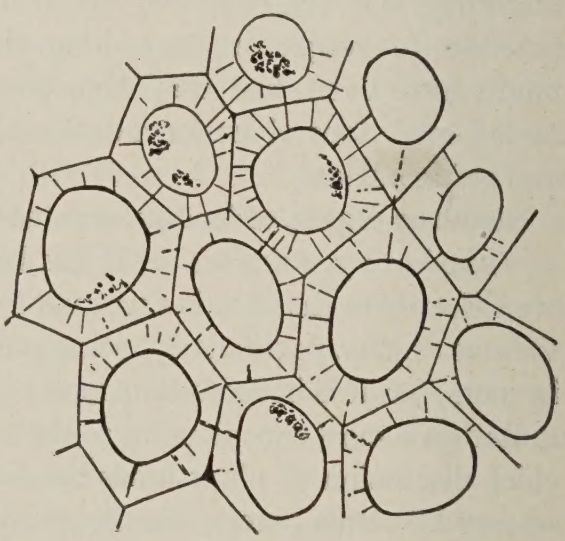


FIG. 515. — A section through part of the endosperm of a persimmon seed (*Diospyros virginiana*), showing greatly thickened walls of "reserve cellulose"; the lines traversing the cell walls indicate the paths of communication between adjacent cells; highly magnified.

[1] All gradations between ordinary chloroplasts and chloroplasts which are reduced to a thin enveloping film often may be seen in the stems of various water plants, as *Myriophyllum*.

[2] However, starch grains exhibit some stratification when exposed during development to continuous illumination.

gins at one end, resulting in eccentric rings (as in the potato tuber, fig. 514). Sometimes more than one grain forms in a plastid, resulting in a compound grain through mutual crowding in growth (as in oats and rice); crowded grains often are polyhedral in shape.

The minute structure of starch grains is in doubt. One view is that they are *spherocrystals*, that is, structures composed of a vast number of needle-like crystals or trichites, radiating in all directions from the growth center. This conception is based upon their behavior in polarized light, which is comparable to that of inulin when precipitated by alcohol (see below). Another view is that starch is an amorphous colloid; formerly this view was supposed to be supported by the fact that starch grains readily absorb stains and swell as they absorb water, but certain undoubted crystals exhibit similar phenomena. Starch grains, because of strains arising from desiccation or otherwise, often exhibit cracks radiating from the center (fig. 324). The exact chemical formula of starch is not known, but it is generally written $n\ (C_6H_{10}O_5)$.

Various non-nitrogenous foods. — Scarcely second in importance to starch among the non-nitrogenous foods in seeds are the *fats* or *glycerides*, which are compounds of fatty acids and glycerine, and are well illustrated in the seeds of the castor bean, cotton, and sunflower, and in many nuts. The fats usually exist as drops of oil in the cell lumina. A third form in which non-nitrogenous food accumulates is the so-called *reserve cellulose* or *hemicellulose*, which makes up the greater part of the thickened endosperm walls of vegetable ivory and of the seeds of the persimmon (fig. 515) and the date; it is " reserve cellulose " that gives the characteristic horny hardness to these and to similar seeds.

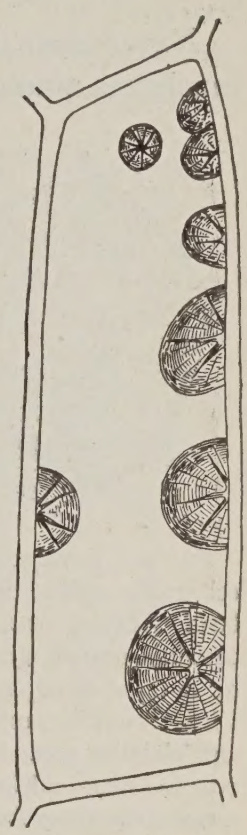


FIG. 516. — A root cell of the elecampane (*Inula helenium*) taken from a specimen preserved in alcohol; note the spherites of inulin with their growth rings and with cracks radiating from the center; note also that where growth begins at the wall, only half of a spherite is formed; highly magnified.

Although they rarely if ever accumulate in quantity in seeds, a word may be said as to sugars and similar substances. *Sugar* (particularly *saccharose* [1]) frequently accumulates in quantity in stems (as in sugar cane) and in roots (as in beets), being in solution in the cell sap. Related to sugar is *inulin*, a carbohydrate occurring in solution in the roots of composites and of various other plants. When these roots are immersed in alcohol, the inulin is precipitated in solid bodies with con-

[1] The sugar of onion bulbs is *dextrose*.

centric stratification layers, as in starch, and also with lines radiating in all directions from the center, suggesting the trichites that characterize spherocrystals (fig. 516). As with starch, the behavior of these bodies in polarized light is that of spherocrystals, yet some investigators still regard them as amorphous colloids.

Nitrogenous foods. — Nitrogenous foods, such as the *proteins*, are much less abundant in seeds than are starches and fats, but they are universally distributed and of much significance. The ordinary protoplasm of the living cells is, of course, nitrogenous; during seed development it is active, but it enters a period of comparative quiescence at maturity, again becoming active at germination. Nitrogenous substances also develop from vacuoles rich in nitrogenous materials and later hardening into *aleurone* grains (fig. 517). In the wheat grain, as in grasses generally, most of the endosperm cells are packed with starch, but the peripheral layer, often called the *gluten layer*, is filled with small aleurone grains (fig. 518); in most other seeds the aleurone grains are scattered among the starch grains or the drops of fat. Sometimes, as in *Ricinus* (fig. 517), the protein grains are large and contain inclusions, such as *protein crystals* and *globoids*, the latter composed in part of calcium-magnesium phosphate. Protein crystals also may lie free in the cell sap, as in the cortex of the potato tuber (fig. 513); such crystals differ from inorganic crystals in being able to take stains and to swell in certain media. In the algae, nitrogenous foods occur in the *pyrenoids*.

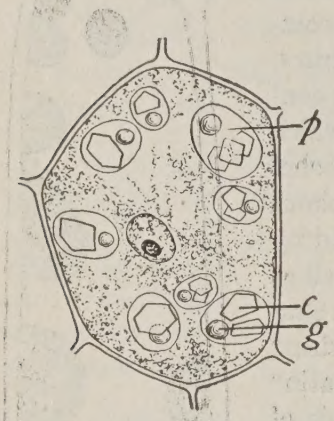


FIG. 517. — An endosperm cell from a seed of the castor bean (*Ricinus communis*), showing protein grains (*p*) made up of amorphous proteins, crystalline proteins (*c*), and globular compounds of protein with calcium and magnesium, the globoids (*g*); highly magnified. — From BARNES.

The distribution of foods in seeds and the associated advantages. — In nearly all seeds there occur nitrogenous and non-nitrogenous foods, the latter always dominating in amount. Commonly one form of non-nitrogenous food dominates in any given case, so that one may speak of starchy, oily, or horny seeds. The percentage of carbon in fat is about 77 per cent, as compared with 44 per cent in starch, yet because of its greater density, a given volume of starch contains about as much carbon as does the same volume of fat. The chief advantage of fatty seeds would seem to be that their relative lightness facilitates

dispersal, while on the other hand starchy seeds are better fitted for quick germination, since the amount of oxygen required to make starch available for growth is much less than that for fat. Thus it is distinctly advantageous that large seeds generally are starchy; where they are not starchy, germination is very slow (as in the coconut). Among the seeds that are slow to germinate are those with "reserve cellulose," as in the date.

The influence of external factors upon the formation of accumulating foods. — Moderately high temperatures are favorable for seed maturation and also for maximum starch production, the optimum temperature for the latter being, in general, in the neighborhood of 25° C. In cold weather, sugar is not readily transformed into starch; indeed, the reverse process often takes place (as in the sweetening of potatoes). An important variable in starch production is the supply of available sugar; if the sugar concentration is high, starch forms more rapidly and at lower temperatures than usual, even at 0° C. Indirectly, light favors starch formation in that it induces a considerable production of sugar, from which starch can be made, but the latter can form in the darkness as well as in the light. The influence of external factors upon the accumulation of fats, proteins, and "reserve cellulose" is not known. For a consideration of food accumulation in tubers and galls, see pp. 234, 298. The rôle of food in seeds will be considered in connection with germination (p. 450).

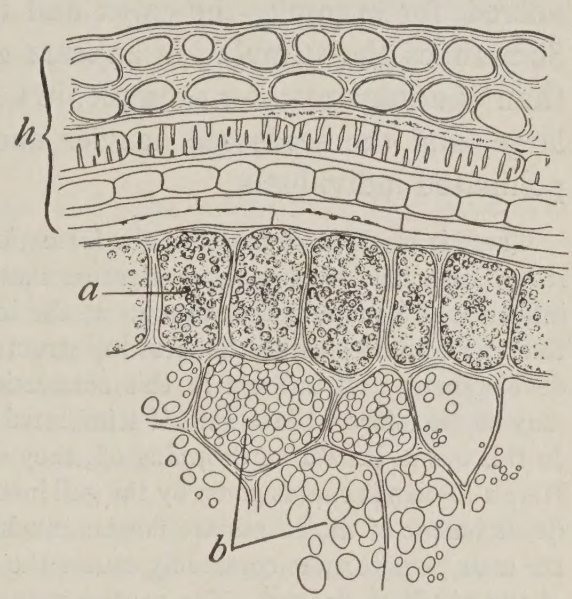


FIG. 518. — A cross section through the outer part of a wheat grain (*Triticum sativum*), showing the husk (*h*) whose outer part is the pericarp and whose inner part is the testa, the aleurone or gluten layer (*a*) whose cells are filled with protein grains, and a part of the starch region (*b*) which makes up the body of the grain; highly magnified. — From COBB.

The structure of the food-containing cells. — Practically all cells in which food accumulates, whether in the endosperm, perisperm, or cotyledons (and also in galls and tubers), are parenchymatic and also are thin-walled except in those cases where the food accumulates in the walls rather than in the lumina as in "reserve cellulose"). There are protoplasmic connections between adjoining endosperm cells, and where the walls are thick, as in "reserve cellulose," the canals containing the connecting protoplasmic threads are quite conspicuous (fig. 515).

Variations in seeds and fruits in relation to external factors. — *The fusion of gametes in relation to fruit development.* — Were the phenomenon not so universal, it would seem amazing that large fruits are

able to develop as a result of so slight an external stimulus as that introduced by a male gamete upon fusion with an egg. In general those pistils in which this fusion takes place develop into fruits, while other pistils show no such changes, soon dropping off, as do the stamens. In the simpler cases fruit development involves only the enlargement or elongation of the ovary, but in other cases various organs may be involved, for example, the calyx and the receptacle (as in the apple). Sometimes the stimulation appears greater in the case of xenogamy than of autogamy; for example, in *Cheiranthus* the fruits are twice as large, and the seeds are heavier and more numerous on the cross-pollinated individuals.

There is much in common in the formation of fruits and galls, and in each case it has been held by some investigators that the growth arises solely through the influence of a momentary stimulus at the inception of the process, and by others that the activities within the growing structures afford constant stimuli for further development. Of interest in this connection is the fact that staminate flowers may be transformed into galls if stimulated by the proper insects (as in the ash). In this event, instead of dropping off, they enlarge and remain for a year or more. Here a foreign stimulus given by the gall insect causes the retention and the further development of the staminate flowers much as another foreign stimulus given by the male gamete more commonly causes the retention and the further development of the pistillate flowers. The precise nature of the fruit-forming stimulus varies considerably with the species. In many cases the act of pollination forms a stimulus of sufficient intensity to inaugurate continued development; this condition is well illustrated in certain orchids in which fruit development has been started by dead pollen or pollen extract placed upon the stigma. In other cases it is the growing pollen tube which initiates fruit development, as in *Geranium* and in various orchids. In the Cucurbitaceae the fusion of gametes is necessary for complete fruit development, although pollination alone stimulates considerable growth. In still other cases the growing ovules are an important stimulus, as in the grape, where the size of the fruit increases with the number of seeds.

Parthenocarpy. — In striking contrast to ordinary fruit production is *parthenocarpy*, or the development of fruit without the fusion of gametes. Familiar illustrations of parthenocarpy are afforded by a number of seedless varieties of cultivated fruits, as in oranges, grapes, and bananas; while only certain varieties of grapes and oranges are seedless, the cultivated banana never produces seeds.[1] In some cases of parthenocarpy, pollination seems to be necessary for fruit development, but it is quite unnecessary in certain figs, where fruit develop-

[1] Plants with parthenocarpic fruits are, of course, propagated vegetatively; it is supposed commonly that they originated suddenly as mutants.

ment occurs without the aid of any known external stimulus. The most striking case of all is in *Balanophora*, a plant which is quite without functional pistillate flowers, but which produces fruits containing viable seeds. In this genus the pistillate flower is reduced to a protuberance with rudiments of a style and an embryo sac. One species (*B. globosa*) lacks staminate flowers, and even in those species which produce pollen, it is, of course, entirely useless, affording one of the best illustrations of the retention by a plant of a useless organ. *Balanophora* is a holoparasite, and it may be that there is some connection between its parasitism and its loss of sexuality.

In recent years the number of plants which are known to be able to develop parthenocarpic fruits has been considerably increased; among such plants are the persimmon, gooseberry, hop, and certain varieties of the apple and the pear. It is also becoming clear that in most cases neither pollination nor any other known external stimulus is necessary to secure fruit development. In several cases, as in the gooseberry and the persimmon, the seedless fruits mature earlier than do the seed-bearing fruits. Obviously fruit production without seeds is wholly useless so far as the perpetuation of the plant is concerned.

Variations in the size and the structure of fruits and seeds. — Probably no other plant organs are as invariable as are fruits and seeds, and for this reason the few variations which are known have an unusual interest. Seeds which develop singly or which are not crowded during development are likely to be spherical, while crowded seeds commonly are angular. In the two-seeded fruits of *Xanthium* and *Cakile*, each seed differs considerably in shape and in size from the other. In certain composites the achenes of the ray flowers and of the disk flowers differ strikingly in shape. In the parasitic Scrophulariaceae it has been discovered that vigorous plants give rise to larger seeds than do weak plants, and that the large seeds give rise in turn to more vigorous plants than do the smaller seeds; furthermore, the larger seeds are more likely than are the others to grow into autophytic individuals, while the plants coming from small seeds in order to thrive, apparently must be parasitic.[1] The achenes of hemp vary considerably in size and in weight, those produced in moist habitats being larger and heavier than those produced in dry habitats. The larger achenes

[1] In this connection it is of interest to note that various parasites (as *Hydnora*, *Rafflesia*, and *Balanophora*) and mycophytes (as *Monotropa* and the orchids) have minute seeds with rudimentary undifferentiated embryos and almost no food, nutritive dependence upon other plants being necessary very early, in most cases even in the earliest stages of germination.

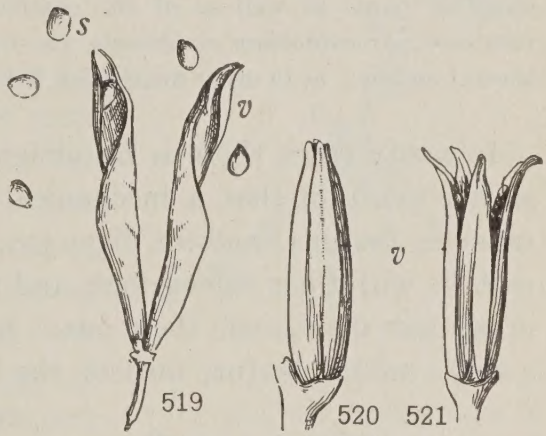
germinate more quickly than do the others, forming stronger plants. Similar differences have been observed in the seeds and seedlings of tobacco. In a crowded group of natural seedlings such a difference in size might be of great significance, since the stronger seedlings would tend to crowd out the others. The influence of grafting upon the character of fruits has been noted elsewhere, but it may be recalled that changes in the size and in the flavor of cultivated fruits often result from the reciprocal influence of the stock and the scion. Pollination may affect the character of the fruit; for example, when the flowers of watermelons are pollinated by cucumber pollen, the resulting fruit is very poor in sugar.

Seed variations manifested in behavior. — Seeds of the same species, though apparently alike in structure, in reality may be very different. Perhaps the best instance of this is seen in a comparison of seeds raised in different climates. Farmers in the United States have long known that northern-grown seeds produce crops that ripen earlier than do crops raised from seeds grown farther south. It appears as if the progeny of the northern plants have inherited from them their short maturation period, thus furnishing evidence in favor of the theory of the inheritance of acquired characters (p. 465). After a few years, however, it is necessary once more to use northern seeds, since the progeny of northern-grown plants come to have the same period that is characteristic of the climate to which they are transferred.

The dehiscence of fruits. — Fruits that open on maturity, thus permitting the ready scattering of seeds, are known as *dehiscent*, while those that do not open are called *indehiscent*. Dehiscent fruits are illustrated by *capsules* (figs. 520, 521) and *pods* (fig. 519), while *berries* (fig. 529), *stone fruits* (*drupes*), and *acorns* (fig. 530) represent indehiscent fruits. Many indehiscent fruits are one-seeded, and may easily be mistaken for seeds; among such are the small, dry fruits, known as *achenes*, especially characteristic of the composites (figs. 524, 527), and also *grains*, *nuts*, and acorns. In the umbellifers the fruits are known as *schizocarps*, the one-seeded carpels splitting at maturity but not dehiscing (fig. 528). Although the habit seems relatively useless, dehiscence occurs in some one-seeded fruits, as in the nutmeg.

Usually the opening of dehiscent fruits is due to an unequal contraction of the pericarp tissues, resulting from desiccation, some cells or tissues losing more water than do others; often the cells are arranged transversely on the concave side, and longitudinally on the convex

side. Capsules usually open in such a way as to expose as many valves as there are carpels, the splitting taking place along the separating walls or along the middle line of the individual carpels. Characteristic pods are illustrated by the crucifers and legumes; among the latter the valves not only are separated by longitudinal splitting, but there may be torsion within the individual valves (fig. 519). Some fruits dehisce through pores, as in the poppy; and in others the lines of dehiscence are transverse rather than longitudinal, resulting in the detachment of the top like a lid, as in *Portulaca* and *Plantago*. At the time of dehiscence the seeds readily become detached from the carpel wall and are exposed to dispersing agencies; the scar left on the seed at the point of attachment is known as the *hilum*. In the pines and in other conifers the cone scales commonly separate from one another at maturity, exposing the winged seeds to the wind; in some species the persistent cones may remain closed for many years (as in *Pinus banksiana*), the seeds thus retaining their viability much longer than otherwise. In some of these trees, extreme desiccation, such as is caused by forest fires, seems necessary to effect the opening of the cones. In some indehiscent fruits there is an outer dehiscent envelope, as in the involucre of the chestnut and the hickory nut and in the aril of the bittersweet.



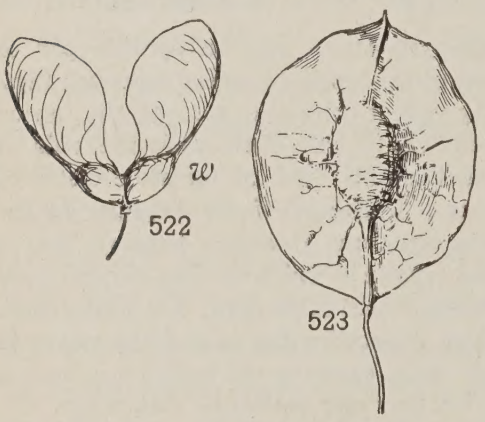
FIGS. 519–521. — 519, an opening pod or legume of the lupine (*Lupinus perennis*), illustrating violent dehiscence through the torsion of the valves (*v*) when desiccated; the seeds (*s*) are mechanically expelled for some distance; 520, 521, dehiscence of the capsules of the evening primrose (*Oenothera biennis*): 520, a mature capsule in which the four valves (*v*) are beginning to split at the apex; 521, a later stage in which desiccation has caused the valves to spread apart, exposing the seeds (*s*) in such a way that they may readily be shaken out.

The dispersal of fruits and seeds. — *Dispersal by propulsion.* — In dehiscent fruits it is generally the seed, and in indehiscent fruits, the fruit as a whole, that is scattered. In some cases the act of dehiscence is so sudden and violent that the seeds are expelled at the same time. At dehiscence the seeds of the violet and lupine are shot out several centimeters (sometimes nearly a meter), while those of the witch-hazel

are expelled much more violently, and may be scattered for several meters. In the lupine the seeds are expelled spirally by reason of the torsion of the valves (fig. 519).

In *Geranium* the carpels separate from the central axis, coiling upwards and discharging the seeds. In *Hura crepitans* the dehiscence is so violent that the seeds are discharged with an explosive report. In *Ecballium* the seeds are squirted out, together with some of the fruit tissues, whence the name squirting cucumber. In *Impatiens* the fruit tissues are in a state of such delicate balance that a mere touch causes violent dehiscence and dispersal, whence the significance of the scientific name as well as of the common name, touch-me-not. In a western mistletoe, *Arceuthobium occidentale*, the ripe fruits explode, ejecting the seeds for several meters; as in other mistletoes, the seeds adhere readily to leaves or bark.

In many cases there is no violent dehiscence, but the seeds lie in such a position that a mechanical impact causes scattering. Most capsules (as in *Oenothera*, figs. 520, 521, and *Pedicularis*) and many pods lie with their valves open, and the wind may shake out the seeds, or animals may brush them out. In many mints, if one presses down a calyx having mature nutlets, the latter shoot out upon release. Of especial interest is *Polygonum virginianum*, whose achene is fastened to an elastic cushion of tissue in such a way that, when pressed back, it bounds off upon release for a distance of three or four meters. Obviously the dispersal of seeds by propulsion is relatively ineffective, since at best the seeds are scattered but a few meters from the parent plant, and commonly much less.



FIGS. 522, 523. — Winged fruits: 522, a samara or key fruit of the mountain maple (*Acer spicatum*): 523, a samara of the hop tree (*Ptelea trifoliata*); *w*, wings.

Dispersal by wind. — With seeds, as with spores, the most effective of dispersal agents is the wind, especially from the standpoint of the number of disseminules carried. As seeds are much larger than spores, the distances covered are much less, though in the case of small seeds, as in the orchids, it is possible that the distances may be very great. Among the commonest of wind-scattered disseminules are those with wings, as in the seeds of the catalpa, and in the fruits (known as *samaras*) of the maple (fig. 522), hop tree (fig. 523), and elm. Such disseminules commonly are much

flattened, and hence are unlikely to fall rapidly to the ground; furthermore, the wings are light, often containing air spaces of considerable size. The wings may be terminal, as in the ash and the maple, or they may form a margin about the seed-bearing portion, as in the hop tree, elm, and bugseed. Similar winged disseminules are found in the pines and birches. In the linden there are relatively heavy, globular, indehiscent fruits, but they are borne on a large, membranous bract attached to the peduncle.

Many wind-scattered disseminules are crowned with hairs. Perhaps the most representative of these are found in the composites, especially in those with milky juice; in the latter, at maturation, the involucre falls back once more as at anthesis, exposing the achenes, with their crowns of hairs (known as the *pappus*) spread out in such a way that the entire structure resembles a parachute (fig. 524); as in parachutes, also, the resistance to the air in falling is considerable, so that wind currents are apt to scatter the achenes for some distance. Dispersal is facilitated still further, if there is a long, slender process (known as the *beak*) separating the achene from the pappus, as in the lettuce and the dandelion, or if the pappus hairs are branched, as in the thistle.

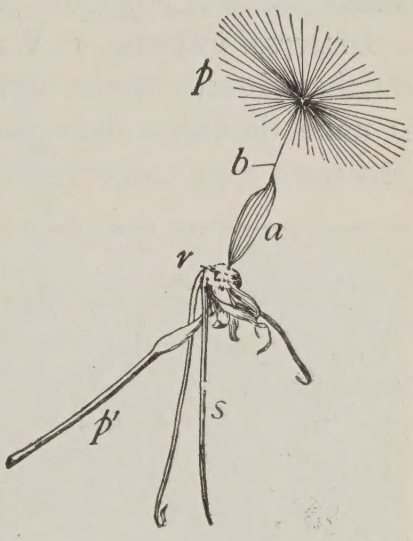


FIG. 524. — A fruiting head of the prickly lettuce (*Lactuca scariola*), from which all of the mature fruits but one have been blown away; note the reflexed involucral scales (*s*) and the achene (*a*), which is prolonged into a beak (*b*) and is crowned with pappus composed of capillary bristles (*p*); *r*, receptacle; *p'*, peduncle.

In the milkweed (*Asclepias*) the seeds bear a crown of long, silky hairs at the hilum end, which enables them to float in the air much as do the achenes of the composite. Similar hairs facilitate dispersal in the willows and poplars, the cottonwood deriving thus its common name. Commercial cotton is derived from the copious hairs that are attached to the seeds of the cotton plant (*Gossypium*); similar cottony hairs are attached to the fruits of some anemones and of the cotton grass (*Eriophorum*).

A remarkable instance of wind dispersal is afforded by the *tumbleweeds*, a class of plants that at maturity break off from the roots as a whole or in part, whereupon they are tumbled along over the ground by the wind, scattering seeds as they go (fig. 525). Among such plants,

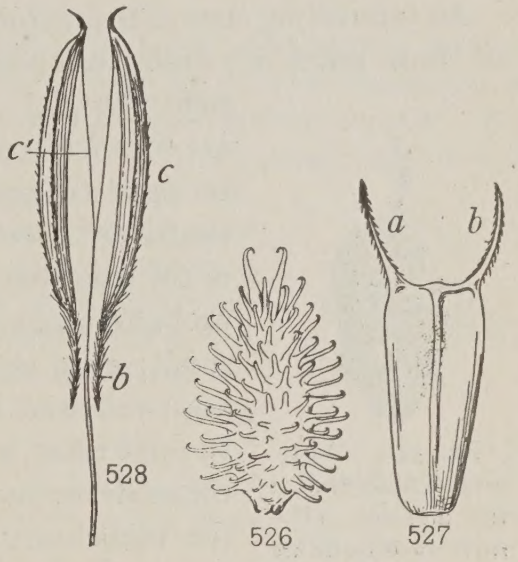
which are especially common on the prairies and plains, are the winged pigweed (*Cycloloma*), the Russian thistle (*Salsola kali tenuifolia*), and *Amaranthus graecizans;* these generally break off entire, but in the old witch grass (*Panicum capillare*) and in some other plants, portions break off and blow about alone or attached to other tumbleweeds.

Dispersal by water. — Water, though less effective than wind in the number of seeds carried to places where they can germinate and grow, is none the less a dispersal agent of great importance, particularly because it may carry disseminules for long distances. Sometimes the

FIG. 525. — A general view of mature plants of the winged pigweed (*Cycloloma atriplicifolium*), a representative tumbleweed; Gary, Ind. — Photograph supplied by MEYERS.

disseminules move in definite directions, as in rivers and in the better-defined ocean currents, but in ponds and lakes the direction of movement commonly varies with the winds. All seeds are heavier than air, and hence are incapable of indefinite propulsion in that medium, but many seeds and fruits are lighter than water, and hence may be carried for great distances; among the latter are the fruits of many water plants and swamp plants, such as *Sagittaria* and *Sparganium*, whose lightness is due largely to the presence of prominent air chambers in the pericarp or testa. Many seeds, however, sink in water, some rapidly and others more slowly, so that the distance they may traverse is more or less limited, as with wind-scattered seeds; among the seeds which sink at once are included those of such pronounced hydrophytes as *Ceratophyllum* and *Subularia*.

Of great significance in connection with water dispersal is the degree of resistance to the entrance of water offered by floating seeds and fruits. Many seeds capable of floating soon lose their vitality through the entrance of water, which thus institutes decay. Particularly is this the case if the water is rough, and more particularly if it is salt as well as rough. For example, the coconut, whose fruit often is seen floating on tropical seas, loses its vitality within a few days through infiltration, so that it is doubtful if it could populate a new land at a great distance, though no illustration of water dispersal is quoted more frequently. In contrast with the coconut are such fruits as that of *Suriana maritima*, a common plant of tropical strands; these have been shown experimentally to be uninjured after floating for 143 days in rough salt water, and the seeds of *Hibiscus tiliaceus* similarly have been shown to be capable of floating for 121 days without injury. The presence of air chambers, especially in the pericarp, greatly retards water infiltration. In *Barringtonia* the resistance to infiltration is so great that broken pieces of the fruit float for more than twenty weeks in a 3 per cent salt solution. The seeds of *Asparagus* may retain their vitality when soaked in water for a year, and in many water plants (as *Sagittaria* and *Proserpinaca*) the seeds may retain their vitality at the bottom of ponds for several years. It can hardly be doubted that in all cases the retention of vitality in immersed seeds is due to the resistance of the various coats to infiltration.



FIGS. 526–528. — Fruits with appendages which become fastened to animals and thus dispersed: 526, a fruit of the cocklebur (*Xanthium*), whose body is covered with stiff recurved prickles; 527, an achene of the bur marigold (*Bidens*), crowned with two sharp and stiff teeth or awns (*a*) which are covered with reflexed barbs (*b*); 528, a mature fruit (schizocarp) of the sweet cicely (*Osmorhiza longistylis*), consisting of two one-seeded carpels (*c*) which separate along the inner face, remaining delicately suspended on slender prolongations of the axis, the carpophore (*c'*); the carpels readily adhere to passing animals by means of the barbs (*b*).

Dispersal by animals. — Many fruits, mainly indehiscent, are scattered involuntarily by animals, particularly the bur fruits and others

with hooked appendages. Unpleasantly familiar fruits of this character are those of the cocklebur (*Xanthium*, fig. 526), burdock (*Arctium*), beggarticks (*Bidens*, fig. 527), hound's-tongue (*Cynoglossum*), sweet cicely (*Osmorhiza*, fig. 528), and bur grass (*Cenchrus*). These and similar fruits are scattered abundantly by man and by domestic animals, and some plants (as *Xanthium*) have thus made a rapid invasion of all continents.

An interesting class of fruits from the standpoint of dispersal consists of those which are fleshy and possess a more or less juicy and edible pulp (fig. 529). Birds and other animals commonly eat such fruits abundantly, often aiding in the scattering of the seeds. Some birds eject the seeds immediately after divesting them of the edible portion of the fruit, but the majority of fruit-eating animals probably swallow the seeds, especially those that are small; even stones as large as those of the cherry are swallowed by animals as small as the raven. In some cases, as in the dove and the domestic fowl, the seeds commonly are destroyed in passing through the alimentary tract. The most useful animals from the standpoint of dispersal are such birds as the robins, thrushes, and blackbirds, which eat fleshy fruits in abundance, swallowing the seeds, and voiding them without harming them in the alimentary tract. Obviously such birds are likely to carry the seeds to some distance from the parent plant, as would not be the case with those that reject the seeds while eating.

FIG. 529. — An aggregate fleshy fruit of the mulberry (*Morus*); such fruits are eaten by animals, the seeds passing undigested through the alimentary tract.

Fleshy, edible fruits when ripe usually are conspicuous by reason of their color, though green and relatively inconspicuous when immature. Of the showy fruits of this sort some are white (as in the snowberry and mistletoe), others red (as in the holly, bittersweet, and cherry), others blue (as in the red cedar and blueberry), and still others black (as in the blackberry and black haw), or yellow (as in various Solanaceae). Though showy fruits doubtless attract fruit-eating animals and thus facilitate seed dispersal, it is likely that the advantage of such showiness has been overestimated. Probably the animals would find the fruits if they were not highly colored; indeed, some edible fruits, as in *Asimina* and *Ribes cynosbati*, are green at maturity. Furthermore, species with fleshy fruits doubtless would become dispersed, even if all

fruit-eating animals should disappear (see below concerning nut dispersal). Showiness, therefore, probably is merely an accompaniment of ripening, indicating the occurrence of certain chemical changes; incidentally they also are of some advantage in that animals thereby are attracted. Some fruits, as the blackberry, are showiest when red and immature, and some showy fruits (as in *Physocarpus*) are quite dry and inedible.

Doubtless various large wading birds, such as the herons, carry seeds in the mud that adheres to their feet, thus accounting, perhaps, for the wide distribution of some swamp plants. Fruit-eating animals do not always facilitate dispersal. For example, in autumn, birds feed abundantly on the fruits of various plants (such as the ragweeds, sunflowers, and certain grasses, as wild rice), eating the seeds, and thus preventing rather than advancing dispersal. It has been shown that ants play an important part in the dispersal of many small seeds, particularly where the seeds have oily appendages which the ants utilize as food. Certain heavy seeds (such as the nuts and acorns, fig. 530) usually are not scattered in any of the above ways; furthermore, they are gathered and eaten in large numbers by squirrels. Occasionally nuts that are carried off by animals are not eaten, and thus may germinate, but at best such a means of dispersal is rather precarious.

FIG. 530. — A nut (acorn) of the black oak (*Quercus velutina*), partially enclosed by its cup (*c*), which has developed from the involucre; note the imbricated scales of the cup (*s*).

The relative efficiency of the various means of dispersal. — Three considerations seem to be involved in successful dispersal: the number of disseminules transported, the distance they are taken, and the degree of precision with which they lodge in places favorable for germination and for subsequent development. Some seeds and fruits are not transported at all, the most notable examples being those that ripen under ground, as in the peanut and in the fruits of the cleistogamous flowers of *Polygala* (fig. 497) and *Viola;* though this habit might seem disadvantageous, no seeds are better placed for germination. A vast number of seeds and fruits have no regular means of dispersal apart from dropping to the ground beneath the plant that bore them; among such are the nuts, the acorns, and many other heavy fruits or seeds. Scarcely more effective are the numerous cases of mechanical propulsion from dehiscent fruits. However, in all these cases the seeds are likely to lodge in places that are relatively fit for germination.

The effective agents of distant dispersal are water, wind, and animals. Water probably is the most likely to carry disseminules for

great distances, but the number of seeds which fall into the water is limited; a great many of these seeds also are injured in transit, and still more fail to lodge in a suitable habitat. Water, however, is of the utmost importance as a transporter of the fruits and seeds of plants which grow in the water, or in swamps, and along shores, since deposition is likely to be in a place that is fit for subsequent growth.[1] Temporary streams, such as torrents following heavy rains, and permanent streams in times of flood, are highly important agents in the dispersal of the seeds of land plants. Wind is the most likely of all agents to pick up and transport seeds and fruits in great numbers from all habitats, but it is also the most indiscriminate of scatterers, depositing all kinds of seeds in all kinds of places, so that the waste of disseminules is enormous. Seeds and fruits scattered by animals may or may not be carried far, but they are likely to lodge in a favorable situation, since animals of a given species tend to frequent similar habitats; wading birds, for example, fly from swamp to swamp, and grazing animals scatter hooked fruits in places similar to those in which they were gathered.

Probably, in spite of its wastefulness, wind is the most efficient of dispersing agents. On newly formed islands the pioneer plants of the interior portions are mainly those whose disseminules are scattered by wind, a smaller number being scattered by birds, while the shore plants are brought largely by water currents. For example, on the island of Krakatoa, whose vegetation was entirely destroyed by a volcanic eruption in 1883, the first plants were thallophytes and bryophytes with wind-borne spores, and the first higher plants to reappear in abundance were ferns, whose spores are readily scattered by wind. Fifteen years after the eruption, fifty-three species of seed plants had reached the island, and of these it was estimated that 60 per cent, chiefly shore species, were brought by ocean currents, 32 per cent by wind, and 8 per cent by animals.

The dispersal of epiphytes is of interest because of the difficulties attending the lodgment of disseminules in places fit for germination. Most epiphytes have wind-scattered disseminules, as in the spores of the lichens, mosses, and ferns, or the seeds of the orchids and bromelias. Most such disseminules are minute, and, while many are wasted, a few find lodgment in bark crevices. The seeds of some epiphytes are scattered by birds, as is the case also with many of the pseudo-epi-

[1] However, the water may carry seeds so far that the new climate is unsuited for development, as in the West Indian seeds carried to the shores of Norway by the ocean currents.

phytes of temperate climates, which occur in soil in the crotches of trees (as the raspberry, gooseberry, and nightshade). Mistletoe, which is parasitic on trees, is also scattered by birds; after eating the enveloping fleshy rind, the slimy seeds which often stick to their bills may be wiped off upon the limbs where they are perched, and hence in places suitable for germination.

A study of the geographic distribution of plants shows that some species, which are known as *endemic*, are confined to restricted areas, and that other species, which are known as *cosmopolitan*, are almost world-wide in distribution; the members of a third class, embracing a much greater number of species, occupy relatively large but not world-wide areas. It might be supposed that the size of the area occupied by a species is determined by its means of dispersal, but this is not obviously the case. While many mobile species (*i.e.* those with easily scattered disseminules) are widely distributed (as in the willows and cat-tails), and while some immobile species are endemic (as in *Torreya*) there are many cases in which the reverse is true; for example, the immobile oaks and beeches are among the most widely distributed trees, while the wonderfully mobile orchids furnish many cases of endemism.

In explaining the distribution of species, many factors other than the mobility of disseminules are to be considered. An important element in the problem is time. For example, even though the oak or beech in a century might be able to migrate only a few meters, in contrast with as many kilometers in the case of the willows, such a difference is of little consequence in the eons of geological time. Hence it may be stated as a somewhat general truth that the rapid occupation of a new area depends largely upon the mobility of plant disseminules,[1] but that this is usually a matter of small moment in determining the ultimate population.[2] Geological history shows that the endemism of *Torreya*,

[1] There are some cases of rapid migration, where the disseminules are not conspicuously mobile, as in *Galinsoga parviflora* and *Artemisia stelleriana*, two composites without the usual hairlike pappus, which have spread over the world in a comparatively few years. Apparently such cases are associated in some way with man, whose various means of transportation seem to have made up, in the case of many species, for any natural lack of disseminule mobility.

[2] Where similar habitats are discontinuous, as in oceanic islands, the flora may be made up for a much longer time than elsewhere of plants with mobile disseminules; the preponderance of ferns in many such places probably is thus explained. Yet even on Krakatoa, a quarter of a century was long enough for the invasion of a number of species with apparently immobile disseminules, whose mode of migration is unknown. It is to be noted that one seed, however extraordinary its mode of migration, may be sufficient to populate a new area with an abundant vegetation.

noted above, is in no wise due to disseminule immobility, for it was once widely distributed, a fact that suggests that the most important of all factors in distribution may be the fitness of a species to exist under the given conditions.

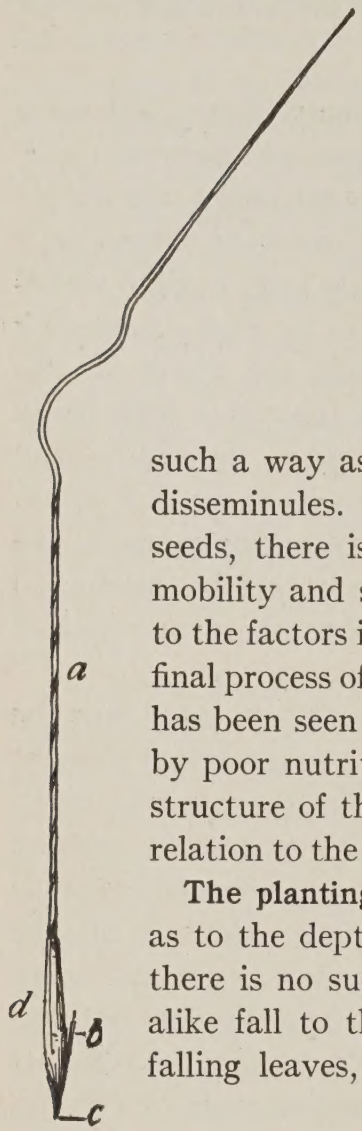


FIG. 531. — A mature fruit of the porcupine grass (*Stipa spartea*), showing the seed-bearing portion (*d*) and the long, spirally twisted awn (*a*); the basal portion or callus (*c*) is stiff and sharp, and is clothed with bristles (*b*) which point upward.

The origin of seed structures. — Nothing is known concerning the factors involved in the origin of the manifold features of seeds and fruits which fit them for the rôle of disseminules. It has been suggested that these features have arisen through natural selection, but such a hypothesis seems incredible in view of the obvious difficulty in grouping seed plants in the order of successfulness in such a way as to show a definite relation to their kinds of disseminules. Even in the annuals, which depend most upon seeds, there is no obvious relation in most cases between mobility and success. Nor is anything definitely known as to the factors involved in seed formation, except that it is the final process of the series initiated by flower formation, which has been seen to be facilitated by xerophytic conditions and by poor nutrition. The seed is by far the most xerophytic structure of the entire series, and thus may bear a definite relation to the causative factors of the reproductive processes.

The planting of seeds. — While gardeners are particular as to the depth at which seeds of various sizes are planted, there is no such sorting in nature. Large and small seeds alike fall to the ground and gradually become covered by falling leaves, by decaying herbage, or by soil that is deposited by winds or waters. Doubtless many small seeds become buried too deeply to permit of successful germination; such a fate is rarer with large seeds, except, perhaps, where they are covered by the deep alluvium of streams. While superficial planting doubtless is more favorable for small seeds than for large seeds, the latter may none the less germinate successfully at the surface; perhaps the chief danger in the shallow planting of large seeds is that there may not be sufficient water for germination.

Seeds that pass through the alimentary tracts of large animals, such as cattle, are planted most advantageously in their excrements, where, upon germination, the young seedlings find an excellent supply of food materials. Nuts buried by animals, if they chance to escape being eaten, often are favorably placed for germination; it is to be recalled also that some fruits mature in the ground (as in the peanut and the violet), so that favorable planting is sure to result. Some seeds and fruits have features enabling them to remain attached to their position on the ground, notably in such hooked fruits as those of the cocklebur and the burdock; in the seeds of flax and mustard the outer layer becomes mucilaginous when moistened, facilitating adherence to the substratum.

A remarkable seed-planting mechanism is seen in certain hygroscopic fruits, notably in the porcupine grass (*Stipa*, fig. 531). Here the fruit is prolonged below into a sharp spine that is clothed except at the tip with hairs that point upward, while above there is a long *awn* whose basal portion coils into a close spiral when exposed to desiccation, and uncoils when moistened, the tissues being so constructed that the evaporation and the absorption of water are unequally distributed. If the spine-tipped base sticks into the ground, the repeated twisting and untwisting of the awn serve to bury it deeper and deeper in the soil, the upward-pointing hairs preventing any movement in the reverse direction. These fruits are such efficient penetrating mechanisms that they work readily through clothes or through envelopes in which they are stored, and penetrate even into the flesh of grazing animals. When the fruits of *Stipa* lie horizontally on the ground, changes of moisture result in a slow creeping movement along the surface. Hygroscopic fruits similar in character to those of *Stipa* are found in various grasses (as *Aristida* and *Avena*) and in *Erodium*, a relative of the geraniums.

CHAPTER VI — GERMINATION

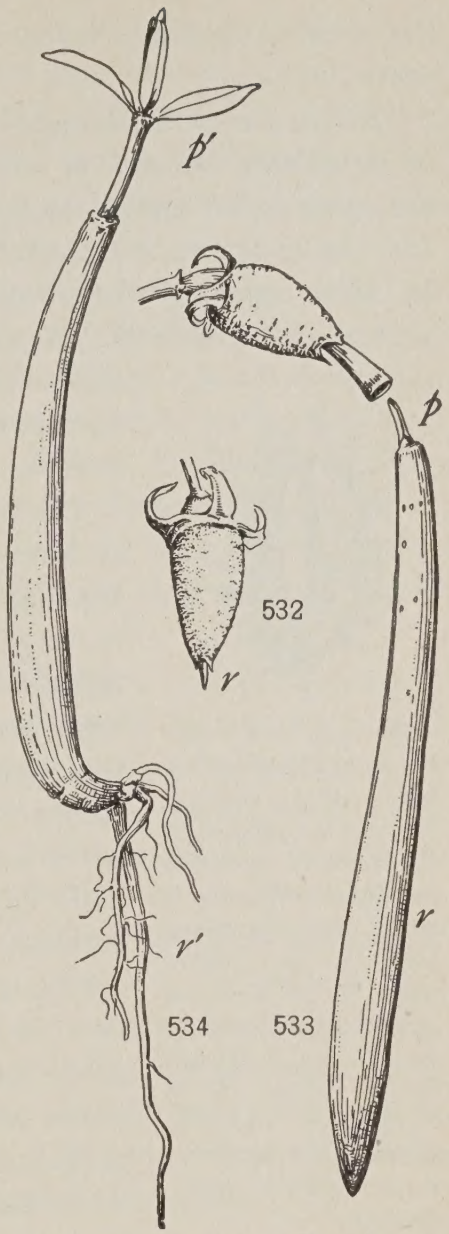
Seed characters that facilitate or retard germination. — *Introductory statement.* — Probably most seeds are able to germinate at maturity, if suitable conditions are present. However, there are many seeds which, under ordinary natural conditions, require the lapse of a longer or shorter period before germination is possible. Such delayed germination may be due to a lack of actual maturity in spite of appearances, or, more commonly, to enveloping structures that retard the germinative processes. There are some seeds which germinate in natural conditions the moment that maturity is reached, the best illustration of such a habit being afforded by viviparous plants.

Vivipary. — *Viviparous* plants are those in which the embryo continues in a state of uninterrupted development from the outset. Since a period of rest between two periods of sporophyte activity is the chief distinguishing feature of the seed, it is obvious that viviparous plants are essentially seedless, and hence do not in the usual sense exhibit germination. The best examples of vivipary are the mangroves (especially *Rhizophora* and *Bruguiera*). In the American mangrove (*Rhizophora mangle*) the " seedlings " develop a large, green, pointed structure, mainly a greatly enlarged hypocotyl, which protrudes from the fruit (figs. 532, 533), and which finally becomes so heavy that the " seedling " drops into the mud beneath; since this structure is heaviest toward the lower end and is much more massive than the plumule, the " seedling " falls right side up into the mud and continues growing, soon striking root and exhibiting vigorous plumule development (fig. 534). Vivipary has been regarded as advantageous to the mangroves, since ordinary seeds might not be able to germinate in the oozy slime beneath the trees. Currents frequently bear the fallen " seedlings " to neighboring shores, so that the viviparous habit also facilitates dispersal; as the young plants float in an erect position, they readily lodge in places which are suitable for further growth.

Seed maturity and germination. — A number of seeds are capable of germination as soon as they are shed; among such are those of the

willows, the sensitive plant, and many cycads, crucifers, and grasses.[1] It is a matter of common belief, however, that most seeds require a resting period of some weeks or months before they are capable of germination, and that in temperate and in cold climates germination ensues only after a period of rest in the ground, coupled with exposure to low temperatures. The real cause of such delay is more likely to be lack of maturity rather than any rest requirement. In many plants the embryo is so imperfectly formed when the seed falls that weeks of development are necessary before the seed is really mature. Here detachment from the carpel does not mean cessation of development but rather its continuation. In *Ginkgo* fertilization does not take place until after the seed has fallen while in some other plants little more than the fertilized egg is present upon the shedding of the seed. Here cell formation continues until the embryo is fully formed and only then is germination possible. In many seeds under ordinary conditions the germinative capacity may improve with age, a certain percentage being capable of germinating after the first winter, a larger percentage after the second winter, and in a few instances a still larger percentage after the third winter; it is said that

[1] It will be recalled that willow seeds soon lose their vitality, especially if desiccated; seeds of the sensitive plant, however, have been known to retain their vitality for sixty years.



FIGS. 532–534. — Vivipary in the mangrove (*Rhizophora mangle*): 532, a mature fruit attached to the tree, the basal portion of the embryo (*r*) just emerging; 533, a later stage in which the young plant has become so heavy that it falls from the parent tree; note the plumule (*p*) and the greatly enlarged basal portion of the embryo (*r*); 534, a stage still later, in which the young plant has rooted freely in the mud (*r'*), the plumule meanwhile having grown vigorously (*p'*).

the seeds of certain conifers are incapable of germination for several years.

This, in some instances, is known to be due to chemical rather than to structural changes in the seeds. Such changes constitute what has come to be known as *after ripening*. In the seeds of the apple and the hawthorn (*Crataegus*) germination will take place only after an after ripening which consists of a considerable increase in the acidity of the embryo. As rather low temperatures favor acid formation this may explain a part of the advantage of "layering," or keeping the seed over winter in moist cool soil.

FIG. 535. — A cocklebur fruit (*Xanthium*) in longitudinal section, showing the position of the two seeds; note that the lower seed (*l*) is larger than the upper seed (*u*) and better placed for germination, since the fruit begins to decay at (*c*); *p*, hooked prickles which aid in dispersal. — After CROCKER (drawn from a photographic reproduction).

The relation of the testa to delayed germination. — Many of the cases of delayed germination of seeds are due to the impermeability of the testa to oxygen or to water. Such impermeable thick testas are particularly abundant among the legumes and the water lilies; notable examples of the former are some of the clovers and the Kentucky coffee tree (*Gymnocladus dioica*) and of the latter the Indian lotus (*Nelumbo nucifera*). This lotus seed has been known to retain its viability for more than two centuries. The common cocklebur (*Xanthium canadense*) has two seeds in each fruit, differing somewhat in shape and in position (fig. 535), and it has been found that the seed nearest the base usually germinates the first spring after maturation, while the upper seed commonly does not germinate until the second spring. In many species some seeds germinate long before others, and it is not unlikely that in some cases the seeds of a given crop may germinate over a period of three or more years. Such a condition seems advantageous, especially in annuals, since it insures the persistence of a species, even though certain seasons prove unfavorable for seed development. In *Xanthium*, it has been shown that the delayed germination of the upper seed is due to the fact that its testa is less permeable to oxygen than is that of the lower seed. In nature the lower seed is exposed first to good germinative conditions, because that end of the fruit disintegrates first. In various plants (as *Abutilon*, *Iris*, and *Axyris*) the

testa (or endosperm) delays germination because it excludes the necessary water. The upper seed in *Xanthium* may be made to germinate early by exposing it to high temperatures (32° C. to 34° C.), probably because the absorption of oxygen and water is thus facilitated; if the testa is removed from the upper seed, it germinates as readily as does the lower seed, and at as low a temperature (22° C. to 24° C.).

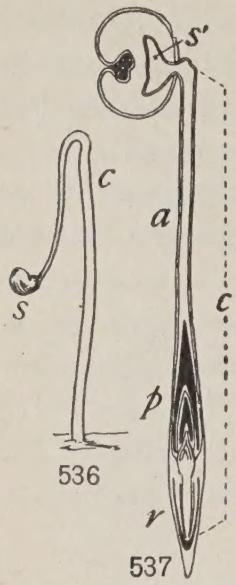
It has been seen elsewhere that the testa is chiefly responsible for prolonged vitality in seeds, and it is here seen to be responsible for most cases of delayed germination. Longevity obviously is advantageous, and to a certain extent delayed germination also may be advantageous, especially in annuals. There is reason to believe, however, that some seeds, especially among xerophytes, are overprotected, the pericarp or testa being so impermeable that death is likely to occur before the water and the oxygen necessary for germination have an opportunity to enter.

The relation of external factors to germination. — It is a matter of common observation that water and moderately high temperatures are necessary for the germination of seeds, and very simple experiments show the equal necessity of oxygen. Nor are any one or two of these factors sufficient. Seeds on a dry shelf never germinate, in spite of favorable temperatures, nor will they germinate in an atmosphere without oxygen or at low temperatures, whatever the other conditions. Oxygen and water appear to be directly necessary for germination,[1] the oxygen being necessary to combine with the accumulated foods, thus making energy for further activity available, and the water being necessary to give the requisite dilution to the cell contents to permit of growth. High temperatures, however, probably are of value only as they facilitate the absorption of water and of oxygen.

The vigorous respiration of developing seedlings is in striking contrast to the weak respiration of seeds, germination soon ceasing in closed chambers from lack of oxygen. The favoring influence of high temperatures is well shown in the date, whose seeds germinate in a few days in a hot greenhouse, otherwise requiring weeks or even months. Formerly it was supposed that germination takes place equally well in light and in darkness. Probably it is true that many seeds are indifferent to the presence or absence of light, but a few seeds require light for germination (as in *Viscum* and in several species of *Rhododendron*); a number of seeds germinate better in light than in darkness (as in *Poa pratensis* and *Veronica peregrina*). On the other hand, there are some seeds whose germination is retarded by light (as

[1] In a few cases, as in rice and in the water hyacinth, no oxygen is required for germination.

in *Phacelia tanacetifolia*). In certain mycophytes and parasites, as previously seen, there is a fourth condition necessary for germination, namely, contact with a suitable host. The exact factor here concerned is not known, though it may be chemical in nature; in certain orchids concentrated solutions may replace the usual symbiotic fungus. Spores in general require germinative conditions similar to those of seeds. Where the spores are green, as in mosses and ferns, light generally is required for germination, though in most cases germination may be induced in the darkness by proper chemical stimulation. Many fungus spores, especially those of parasites, germinate readily in water, but the spores of many saprophytes require for germination the presence of a nutrient medium.



FIGS. 536, 537. — Monocotyl seedlings: 536, an onion seedling (*Allium cepa*), illustrating epigaean germination; note the curvature of the cotyledon (*c*) whose tip remains within the seed (*s*), acting as an absorptive organ; 537, the seedling of a date palm (*Phoenix dactylifera*) in longitudinal section; note the remarkable cotyledon (*c*) whose axis elongates upon germination; one end of the cotyledon (*s'*) remains within the seed, acting as an absorptive organ; the other end continues for a time to enclose the plumule (*p*) and the radicle (*r*). — From KERNER.

The germinative processes of seedlings. — *Initiatory activities.* — In those seeds in which the outer layer becomes transformed into mucilage upon the absorption of water (as in flax and mustard), this is the first germinative phase to be observed. Very soon the seed swells noticeably, owing to the large amount of water absorbed. The outermost cells become active, as soon as their contents become sufficiently dilute; diastase or other enzymes are secreted, and the digestion of the accumulated food begins. When the water and the transformed foods reach the embryo and incite it to its second and final period of activity, germination proper may be said to have begun.

The digestion and the absorption of foods. — The digestive processes are observed readily in the grains of cereals, as in wheat. The aleurone layer (fig. 518), which is rich in protein, first shows signs of life, the cells becoming large and vacuolated and the protoplasm manifesting activity. Soon the secretion of diastase begins, and the starch next to the aleurone layer is the first to be digested. In wheat, maize, and other grasses there is a specialized structure, the *scutellum* (structurally the cotyledon), which greatly facilitates the germinative processes, since it serves as a path of transfer for the digested foods from the endosperm to the developing embryo; often on the side next to the endosperm there are hairlike absorptive

cells. In many monocotyls the tip of the cotyledon remains in the seed in contact with the food and may be regarded as an absorptive organ (fig. 536). In the date the tip of the cotyledon enlarges into a disk, presenting a large absorptive surface to the endosperm (fig. 537). In those seeds in which the accumulated foods are in the cotyledons, specialized absorptive structures are less likely to be present.

The amount of food in seeds may vary from almost none (as in many parasites and mycophytes) to such large quantities as are found in the coconut and the avocado (*Persea gratissima*). In cases like the latter, much or little of the food may be utilized, depending upon the conditions to which the seedling is exposed upon emergence from the testa. If the radicle has ready access to moisture and the plumule to light, most of the food is unnecessary and may gradually decompose in the ground; but if conditions for autophytic nutrition are less favorable, much or even all of the food may be used by the seedling.

Aspects of germination external to the seed. — The earliest conspicuous external index of germination is the rupture of the testa and the protrusion of the embryo. The time necessary for such protrusion, after the seeds have been exposed to proper germinative conditions, varies from one or two days (as in lettuce or mustard) to some weeks or months (as in the date). Small seeds germinate more quickly, as a rule, than do large seeds, probably because the foods are digested more quickly through easy access to water and oxygen. Starchy seeds commonly germinate more quickly than do fatty seeds, and much more quickly than do seeds with " reserve cellulose." The rupture of the testa, which usually becomes much softened and weakened by the absorbed water, may be effected by the growing radicle or by the cotyledon, as in many monocotyls. Sometimes the embryo emerges through thin spots, as in the coconut, or pushes out a loosely fastened plug of tissue. Usually the radicle is the first part of the embryo to protrude, and this is doubtless advantageous, since most seeds contain enough food for considerable growth, while all of the water must come from without. Often (as in the cocklebur) the radicle is so situated that it is the first part of the embryo with which the entering water comes in contact,[1] and the absorption of water from the soil by the young root system usually is well initiated before the external development of the plumule becomes prominent.

[1] The significance of the position of the radicle in the seed of the cocklebur is seen from the fact that if a bit of the testa is removed near the tip of the cotyledons, growth begins at that point, the radicle then being the last part to react.

In some cases the cotyledons remain in the soil, especially where these organs are the chief seat of accumulated food, as in oaks and peas, and also in the cereals, where the scutellum represents the cotyledon (figs. 4, 7); such germination is termed *hypogaean*. In other cases the cotyledons emerge from the seed with the plumule and come into the light, usually turning green, as in the beech (fig. 538), pumpkin, and mustard (fig. 1); such germination is termed *epigaean*.

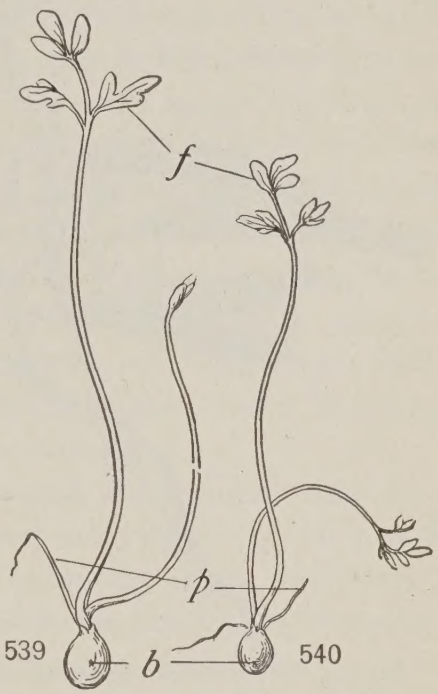
FIG. 538. — A seedling of a dicotyl, the beech (*Fagus grandifolia*), illustrating epigaean germination; *c*, cotyledons; *f*, first foliage leaves.

In hypogaean species the cotyledons die, as soon as the foods are removed, or the seedling is well established as an autophyte. The same is true in some epigaean species, as in various beans, but in many other epigaean forms the cotyledons enlarge and doubtless manufacture considerable food. Cotyledons are much more uniform in shape than are ordinary leaves, perhaps because of the relatively uniform conditions in which they are developed. Usually they are undivided, though occasionally divided, as in *Tilia*. In the monocotyls the enclosure of the delicate part of the plumule within its older sheathing leaves prevents injury in breaking through the soil. In many epigaean dicotyls the cotyledons adhere at the tips, protecting the plumule until it emerges from the ground. In other cases (as in the pumpkin) the hypocotyl elongates considerably, while the cotyledons remain within the seed, resulting in an arching of the young stem and in the pulling of the delicate tip from the seed and through the ground instead of pushing. Where seeds germinate too near the surface, the contraction or other movement of the growing root exerts a pull on the shoot, so that the position proper to the species is eventually acquired.

The germinative processes of buds. — *The structural features of buds.* — Buds commonly are divided into two classes, *active* and *resting*. Active buds are associated with all seasons in uniform climates and with the vegetative seasons of periodic climates, while resting buds are associated with the unfavorable seasons of periodic climates. Germinative processes are conspicuous as resting buds develop into active buds. The resting buds of shrubs and trees, commonly called *winter*

buds in temperate and in cold climates, are protected by tough and impermeable bud scales, whose structure and rôle have been considered elsewhere (p. 157). Within the bud scales are delicate embryonic leaves that are most economically arranged as to utilization of space, a particular kind of arrangement, known as *vernation*, often being characteristic of special plant groups.

Leaves in the bud may be *plane; conduplicate*, or folded inward, as in the bean; *plicate*, or folded in pleats, as in the beech; *crumpled*, as in the poppy; *involute*, or with the halves rolled inward, as in the violet; *revolute*, or with the halves rolled outward, as in the dock; *convolute*, or with the leaf rolled from one margin to the other, as in the canna; or *circinate*, that is, with the leaf rolled inward on itself from the apex downward, as in ferns. It is believed that the kind of vernation is due in part at least to the limitations of space within the bud; by experimentally restricting this space, the leaves of *Prunus* which usually are flat become crumpled, and by cutting the stipules, the leaves of *Magnolia* become flat.



FIGS. 539, 540. — Bulblings of *Cicuta bulbifera;* the first bladeless leaves or phyllodes (*p*) are followed by foliage leaves (*f*); *b*, bulbil.

External factors in relation to bud germination. — The germination of winter buds is associated largely with spring, and, as with seeds, it takes place when the temperature becomes sufficiently high to permit water to enter the embryonic shoot in abundance and to incite it to activity. Buds differ from seeds in being embryonic shoots rather than embryonic plants, and usually also in remaining attached to the plants that bear them (except in the winter buds of water plants), the water used in germination thus coming from the plant rather than from the ground. As shown elsewhere, buds often appear to be mature before they are capable of germination, the maturation process seeming to consist in part in the accumulation of food. Germination may be hastened by placing a plant or even a branch indoors in winter. Only local stimuli are needed for germination, as is shown by growing a single branch detached from a plant and placed in water indoors, or

by training a branch from a tree into an adjoining house, or even by supplying favorable temperatures locally to a part of a plant outside, as by bending a willow branch into a sheltered position; because of locally favorable temperatures, buds germinate soonest on sunny slopes, and willows on the tundra come into flower while their roots are still in frozen soil. The resting buds of herbaceous plants, represented by bulbs and bulbils (the latter developing into *bulblings*, figs. 539, 540), and by the buds of tubers (fig. 344), of rhizomes, and of multicipital herbs, germinate under conditions similar to those that incite activity in the resting buds of trees and shrubs.

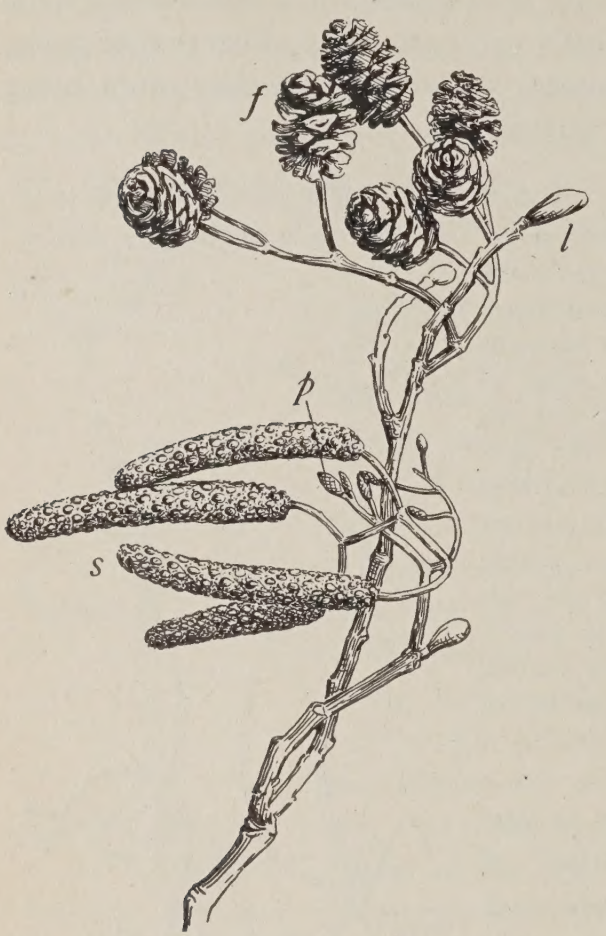


FIG. 541. — A branch of the European alder (*Alnus glutinosa*) in its winter aspect; *s*, the buds of staminate inflorescences; *p*, the buds of pistillate inflorescences; *f*, fruit cones of the preceding year; *l*, leaf buds.

Climate and bud development. — As a rule, trees and shrubs with large buds (as the poplars, willows, and alders, fig. 541) develop vigorous shoots early in spring, while species with small buds (as the catalpa and the honey locust) develop much later. Such differences seem to follow from the fact that in the former the embryonic shoots are much the more advanced while still within the resting bud. Many of the large-budded forms which thus develop at the inception of spring are northern species, and such habits seem very advantageous for far northern plants, owing to the shortness of the vegetative season. On the other hand, where the vegetative season is long, small buds seem advantageous, owing to their exemption from the development of extensive protective structures. Some large-budded trees, such as the hickory, are both late in germinating and relatively southern in distribution.

CHAPTER VII — PLANT COMMUNITIES

Definition. — In the preceding chapters, plants have been considered as individuals having certain relations to their physical surroundings, or to each other. While plants sometimes occur as isolated individuals, they are associated far more commonly in more or less definite groups. So true is this that when one who is familiar with nature sees a given species in the field, he comes almost instinctively to look for other species that he has seen associated with it. If he is observant, he looks a step further and finds that these associated species also are associated with a definite kind of habitat. For example, pitcher plants, sundews, cranberries, and peat moss grow together in imperfectly drained swamps known as bogs or moors; beach peas, sea rocket, and beach grass grow together on sandy coasts; beech, maple, beech fern, and beech-drops grow together in mesophytic forests.

A group of plants in its entirety occurring in a common habitat is known as a *plant community*. Sometimes the association of specific plants in the community is obligate, as in the case of the beech-drops, which grows parasitically on the beech, while the beech in turn appears to require certain fungi in the soil which form its mycorhizas. More commonly, however, the association is partly or completely facultative. Many herbaceous plants such as the baneberry, beech fern, and wild geranium, require the close association of trees to furnish the shade in which they thrive. Pitcher plants and sundews or beeches and maples grow together, because they thrive in similar conditions; so far as known, the presence or the absence of one is a matter of no particular consequence for the other except as it occupies or leaves a certain amount of space.

The kinds of communities. — Various ranks of plant communities have been distinguished but no general agreement has been reached, as yet, regarding how many such ranks shall be recognized. It is generally agreed, however, that the *plant association* should be one of the first to be recognized and investigated. A plant association may be defined as a plant community with definite floristic composition. It

has also definite ecological structure and develops under uniform conditions of habitat. A forest dominated by beech and maple trees, with a rather definite aggregation of plants in the undergrowth, would constitute a *beech-maple forest association.* Such associations may be regarded as entities possessing individual characteristics, within which the various plants exhibit phenomena of priority, competition, dependence, and mutuality.

Many of the conditions within such plant communities resemble so closely those within human communities that their study has, at times, been termed *plant sociology.*

Various plant associations possessing common characteristics may be grouped into communities of higher rank and wider extent designated as *plant formations.* Thus forests of beech, maple, oak, hickory, and chestnut form the *deciduous forest formation* of North America. Similarly plant associations may be divided into smaller units termed *plant societies* and the spring flowers of the beech-maple forest association constitute one or more *herbaceous plant societies.*

Without doubt the first classification of plant communities was made long before ecology was recognized on the basis of their physiognomy as expressed in the various growth-forms composing them. When trees dominated the community a *forest* resulted. When shrubs determined the aspect of the vegetation *scrub* communities resulted; when trees and grasses mingled a *savanna* was formed, while with the absence of trees the grass-covered area became a *prairie.*

The simplest grouping now used by ecologists is based on the water relation and the large divisions are termed *hydrophytic*, *mesophytic*, and *xerophytic*, while these in turn are subdivided into various groups of communities. This classification, though advantageous because of its ready application, has the great disadvantage of grouping together associations that are entirely unrelated in origin, such as those of bogs and ordinary swamps, while separating closely related communities, such as those of bogs and of the coniferous forests into which they commonly develop. Though it is more difficult to apply, there are many advantages in a genetic classification, that is, one which groups communities in a series in their order of development.

Succession. — The basis of a genetic classification is the principle of *succession*, namely, that in the physiographic development of a region the various habitats pass through a series of more or less definite stages, owing chiefly to the processes of erosion and deposition, supplemented

by the accumulation of humus. The primitive communities, that is, those of new lands or waters, are likely to be either xerophytic or hydrophytic. In a region with a mesophytic climate, the primitive communities become displaced by others that are slightly more mesophytic, and they in turn by others, until the series finally culminates in the most mesophytic community of which the region as a whole is capable. For example, in the eastern United States an upland of rock, sand, or clay, whose original flora is xerophytic, becomes gradually more and more mesophytic, either through land denudation or humus accumulation or both, until it becomes clothed with the ultimate plant community of the region, namely, a deciduous mesophytic forest. A pond in the same region gradually becomes filled through humus accumulation or through stream and shore deposition, or both, so that the original aquatic vegetation becomes displaced by a swamp vegetation, and this in turn through further humus accumulation becomes displaced by a forest quite comparable to that which marks the final stage in an upland succession. In arid or semi-arid climates it is obvious that the final stage could not be mesophytic, but would necessarily be a community which is much nearer the primitive xerophytic community of the region.

The scope of this book forbids any attempt at a detailed classification of plant communities. The general principles enunciated above must suffice. In the remaining paragraphs of this chapter there will be presented some of the more striking features of a few of the more important plant communities, especially of those that are found in the United States, but no attempt will be made to bring out genetic relationships or to make exhaustive analyses.

Pond communities. — Perhaps the most representative fresh-water communities are those of ponds, and these are among the most interesting of all associations, partly because they are more likely to remain natural than are most habitats in densely populated districts, but especially because they show obvious and rapid stages in succession between the primitive aquatic communities and the various sorts of swamps. The vegetation of ponds consists usually of free-floating forms (including many algae and some higher plants) and of forms attached to the bottom; of the latter some forms are submersed, some have floating leaves, and still others are in part emersed. Aquatic plants or hydrophytes, especially those that are submersed, have many noteworthy structural peculiarities that have been separately noted on previous pages, but which may here be summarized.

The root systems commonly are reduced, both in length and in amount of branching, and root hairs are absent, at least in the water. True water roots are hairless, and may possess root pockets. The chlorenchyma is spongy and but slightly differentiated, and usually the plastids are large and motile. The leaves of submersed plants are very thin and often are finely dissected. Air chambers are capacious, often exceeding the tissues in actual volume. Stomata are absent in submersed leaves and are present only on the upper surfaces of floating leaves; where present in floating or in emersed leaves, they have but slightly cutinized walls and are almost always open. Protective features are few or wanting; for example, cutin and cork rarely are developed below the water surface, hairs are scarce, and the cell sap has a low osmotic pressure; the absence of protective structures is not disadvantageous, since absorption is easy, and below the water level transpiration is slight or even absent. Leaves equal or surpass roots in importance as absorptive organs. Submersed organs usually are slime-covered, the slime harboring commensalistic communities of bacteria and other low organisms. The aerial surfaces of floating organs usually are wax-coated and thus are not readily wetted. Conductive and mechanical tissues are greatly reduced. Vegetative reproduction is highly developed, both through the fragmentation of ordinary shoots, and through the development of winter buds. In the algae, reproduction and dispersal are facilitated by zoospores and by motile gametes. Among the higher plants, flowers and seeds are less abundant than in most habitats.

Swamps. — Various swamp stages in turn follow the primitive pond associations, bulrushes, cat-tails, and reeds often being among the first emersed plants, and sedges are often prominent later. In mesophytic climates, thickets (as of willows and alders) soon appear, and they in turn are replaced by forest vegetation. The structural features of swamp plants are in part like those noted above, especially in the matter of reduced root systems and prominent air chambers, but in general they are not unlike those seen in mesophytes; particularly is this true of leaf thickness, stomata, chlorenchyma, and protective structures. The roots frequently are horizontal or even ascending rather than descending. Rhizomes are greatly developed, accounting in large part for the rapid invasion of ponds by swamp plants. A somewhat remarkable feature is the abundant development of vertical chlorophyll-bearing organs, whether leaves (as in the flags) or stems (as in the

rushes). Among the most plastic of plants as to leaf form and structure are the amphibious plants; in view of the rapid transformation of ponds into swamps, such plasticity permits certain species to dominate in two distinct successional stages.

Bogs or moors. — The mature vegetation of a peat bog contrasts strikingly with that of an ordinary swamp, although the early stages may be quite the same in both cases. While a number of plants are common to swamps and bogs, there are many kinds of plants which are more or less peculiar to bogs, the most noteworthy being those with such xeromorphic features as prominent palisade tissues and cutin, dwarfness of habit, and high osmotic concentration of the cell sap. Among bog xeromorphs are many ericads (such as the cranberry, leather leaf, and Labrador tea) and conifers; that some of the bog plants are true xerophytes is shown by the fact that a number of species are common to bogs and to dry rocky cliffs. It has been suggested that the xeromorphic peculiarities of bog plants may have developed elsewhere and that the plants afterwards migrated to the bogs. Plants from without, when grown in bog conditions, develop a weak root system and xeromorphic leaves, facts that make it probable that most bog plants owe their xeromorphic peculiarities to their sparse root system and this in turn may be due to the high acidity and the lack of oxygen in the bog itself.

Certain mosses, notably the peat mosses (*Sphagnum* spp.) are especially characteristic of bogs, as are many orchids, and it is in bogs that most carnivorous plants are found. As compared with mesophytic habitats or with ordinary swamps, bogs present conditions that are deleterious for the majority of plants; indeed, some plants which are characteristic of bogs, notably the tamarack (*Larix*) and the black spruce, thrive much better elsewhere, suggesting that they "tolerate" bogs rather than "select" them. Such trees probably grow in bogs because they do not there find the competition which they meet elsewhere.

Maritime communities. — Plants that grow in salt water or in salty soil have been denominated halophytes. The submersed halophytes are chiefly algae, which sometimes reach gigantic size, and which differ in color, being green, red, or brown. Most of the larger algae are attached to rocks by anchoring organs, namely, the holdfasts or rhizoids; some rise and fall with the tide, bladders filled with air often facilitating their buoyancy. Salt marshes show stages in succession comparable to

those of ponds, but the species involved are very different. Emersed halophytes are strikingly xeromorphic in their characteristic features, palisade tissue being prominently developed, and often the epidermis is highly cutinized. The most striking feature of salt marsh halophytes, taken as a class, is their succulence, which is accompanied by a very high osmotic pressure. In temperate regions the most representative salt marsh plants are herbaceous, but in the tropics extensive mangrove forests are found in similar conditions; few plants show more marked xeromorphic features than do the mangroves, which have evergreen leaves with water tissue, prominent palisade cells, and thick cutin. Often there is a network of prop roots above the water line, and in some cases there are ascending " knees " (fig. 27).

Xerophytic communities. — *The characteristic features of xerophytes.* — In most respects xerophytes are the reverse of hydrophytes in their structural features. The roots frequently are strongly developed (though not in cacti), possessing either considerable length or great size; roots of the latter class accumulate large amounts of water and food. In some extreme xerophytes the root hairs extend to the root tips, and in certain cases they possess rigid thickened walls. Palisade tissue is strongly developed, and the chlorenchyma in the leaves and stems commonly is deeply sunken, giving them a pale tint as viewed from without; usually the plastids are small and relatively immotile.

Protective features are remarkably developed both in amount and in kind, and their advantage is undoubted, owing to the great exposure of xerophytes to transpiration. The transpiring surface usually is relatively reduced, the leaves being small and thick. Many species are leafless, the cylindrical stems exposing a relatively small surface to transpiration, while their vertical orientation affords some protection from the intense rays of light at midday; species with vertical leaves are similarly protected. In many cases there is a temporary reduction of surface, as in the involute leaves of grasses, as in those legumes whose leaves close in dry weather, and as in the " resurrection plants." Temporary reduction of surface is exhibited also by plants which shed their leaves or stems during dry periods; annuals, which die at the beginning of dry periods, represent the culminating form of such behavior. Dwarfness of habit is a prominent xerophytic feature, the resulting compactness in arrangement of branches and leaves and the closeness to the ground affording considerable protection.

The more minute structural features of xerophytes are no less significant than are the more obvious characters. Commonly the epidermis is thick and highly cutinized (except in succulent xerophytes), and often it is superficially coated with wax, resin, or varnish. In woody stems there is a prominent bark development, the cork in particular being of high significance in checking transpiration. The leaf and stem surfaces frequently are covered with hairs; spinescence also is common, though its protective significance may not be important. The stomata occur mainly on the more protected (chiefly the under) surfaces, and often are at the bases of pits and especially protected by hairy coats or by cutinized walls; as a rule, they are not wide open. Many xerophytes are succulent, containing large amounts of colorless sap or of latex; oils and resins often are abundantly developed. The osmotic pressure of the cell sap often is very high, especially in shrubs and in plants of alkaline soil. The conductive tracts are prominent, the vessels being larger and longer and the walls thicker than in most plants; lignification is prominent, and annual rings are well developed. Bast fibers and other mechanical elements reach their highest development in xerophytes.

Some xerophytes, particularly the lichens, appear wanting in prominent xeromorphic structures, seeming able to withstand prolonged desiccation without injury. Apart from the lichens and mosses, absorption through aerial organs is relatively rare in xerophytes, though some of the epiphytic leaf-absorbing bromelias grow in dry climates. Tubers, corms, and bulbs especially characterize arid climates, and it is obvious that their ability to develop rapidly at the inception of a rainy season is a character of great advantage. Xerophytic conditions usually are believed to favor the formation of flowers and fruits.

Characteristic xerophytic communities. — Perhaps the most representative xerophytic region is the desert, and it is here that the features above mentioned reach their most pronounced development. In general the severity of the desert conditions increases as the rainfall decreases, it being common to distinguish half deserts, such as the sagebrush plains, from the more extreme deserts, such as those in which plants like the cacti, or the creosote bush, are dominant forms. Still more extreme are the alkali deserts, in which excessive climatic aridity is supplemented by a soil in which concentrated salts make absorption difficult. Succulents with sap of high osmotic pressure seem

best fitted for existence under such conditions. There are habitats where the alkalinity is so great that plant life is almost if not quite excluded.

Many, but not all, alpine and arctic habitats have plants whose structures are chiefly xeromorphic. Even though there is an abundant supply of water, the soil often is so cold that absorption is difficult; consequently plants without xeromorphic structures are poorly fitted for such habitats, except in alpine meadows or in similar situations, where the protective mantle of snow prevents the loss of water by transpiration in the seasons during which absorption is impossible. The leaves of alpine and arctic xerophytes are largely sclerophyllous, hairy leaves being rather less abundant than in deserts. The perennial habit is almost universal, the shortness of the season scarcely permitting annuals to complete their life cycle. Anthocyanins are prominently developed, resulting in showy leaves and flowers. Palisade tissue is more pronounced in alpine than in arctic xerophytes.

In climates where the rainfall and the temperature are such as to facilitate their development, there are many habitats where the local conditions prevent for a time the appearance of mesophytes. Among such habitats rocky and sandy areas are of first importance. In rocky regions the pioneer plants often are lichens, which are able to grow on the bare rock surface; with these come many crevice plants. By the accumulation of humus, the growth of other plants is made possible, and after a time a thicket develops, and later a forest, in which pines and junipers may play an important part. In sandy regions the instability of the soil usually inhibits the development of a pioneer lichen stage, whereas xerophytic herbs and shrubs make their appearance sooner than on rocks. The subsequent stages on rock and sand are much the same.

Mesophytic communities. — Mesophytes in their structural characteristics are in many respects intermediate between hydrophytes and xerophytes. There is a prominent development of progeotropic roots with abundant root hairs. The foliage reaches a maximum development, and the leaves are relatively large and thin, while the thin transparent epidermis and the abundant chlorophyll together cause the leaves to appear dark green. Stomata usually occur on both leaf surfaces, except in trees, and the guard cells possess a maximum capacity for movement. Cutinization is moderate, except in such evergreens as the hemlock and the India-rubber tree. The under epidermis com-

monly has wavy lateral walls, contrasting thus with the straight walls in hydrophytes and xerophytes.

The most representative mesophytic communities are, on the one hand, various forests, and, on the other, certain grasslands. The mesophytic forests as a class are the culminating vegetation of any region where they grow, since they represent not only the most luxuriant kind of plant community, but also because they form the terminal member of the successional series in such climates as are humid enough to support them over extensive areas. It is in the mesophytic forests that humus accumulation above the water level reaches its maximum, and on this account the soil is more uniformly moist than in other land habitats. Furthermore, the rich supply of humus makes possible a wealth of saprophytic fungi and bacteria, leading to mycosymbiosis and to other symbiotic relations.

The most luxuriant of mesophytic forests is the rain forest of the tropics, which is characterized by the dense crowding of individual plants, resulting in the maximum occupation of space. Not only are there ordinary trees, shrubs, and herbs, but lianas often are abundant, while epiphytes cover the limbs and even develop on the leaves of many trees. The trees often are slender and smooth-barked, and the leaves are characteristically evergreen. The epiphytes include ferns and orchids, the latter with characteristic absorptive roots and xeromorphic leaves or stems; the leaves of many of the trees appear xeromorphic also. In north temperate regions there are extensive mesophytic forests that either are deciduous, as in the eastern United States, Europe, and Japan, or evergreen, as in the northwestern United States. In these forests the tree species are relatively few in number, as compared with the tropical forests, and the trees often are large and rough-barked. The epiphytic vegetation consists chiefly of lichens, liverworts, and mosses. Frequently mesophytic areas are treeless, as in some prairies and in alpine meadows, where grasses and herbage dominate the landscape.

The influence of man upon vegetation. — Man is the most destructive of animals. He has cleared vast tracts of forest for lumber, and for the building of cities and the development of farms, and has destroyed other tracts through forest fires. Man also is responsible for distributing through the world most of the " weeds " which burden the farmer and throng the roadsides. Such plants as the Russian thistle, cocklebur, burdock, and Canada thistle once were somewhat restricted

in area, and they owe their present widespread distribution directly or indirectly to man. Plants of this sort that inhabit fields and waste places are known as *ruderals*. Often there are ruderal communities, such as those that develop on cultivated land that is left fallow. The pioneer communities that follow in man's destructive train, such as the ruderal communities of fallow land or the " fireweed " communities of a burned forest tract, usually are comparable to pioneer associations of xerophytic tracts, and often they contain xerophytic species. If man leaves such areas to their natural course, there is a succession of communities comparable to those previously noted, culminating finally in the plant community that originally dominated in the region.

CHAPTER VIII — ADAPTATION

The problem of adaptation. — In the preceding chapters it has been seen that most plant structures are more or less perfectly suited for the conditions in which they live, and that their behavior is in most instances advantageous. There have been various theories to account for the origin of the obvious harmony between plants and their surroundings. Originally it was supposed that plants were *specially created* with the structures and behavior that they now possess, but it has long been known that their characters are the result of evolution.

The theory of adaptive response. — A common theory, prevalent especially in the past century, has been that plants possess an inherent capacity to *adapt* themselves to their surroundings, being able as conditions change to change their structure or behavior or both in an advantageous manner. Indeed, this doctrine has been formulated into a so-called law, namely, that the cause of a need is at the same time the cause of its satisfaction; new conditions create new needs, and the new needs are supposed to result in new organs.[1] For example, the abundant development of root hairs in a moist air culture of maize seedlings has been regarded as an *adaptive response*, the hairs being believed to grow abundantly because they are needed, whereas water cultures of the same species are thought to be hairless, because hairs are not needed in a water medium. Such a philosophy, in which need is supposed to control response, and in which, therefore, the pursuit of material causes is replaced by purposive expressions, is denominated *teleological*.

The theory of adaptive response has had two aspects; some investigators hold that plant species remain plastic and thus able to adapt themselves directly to changed conditions, while others hold to a theory of original plasticity, with the subsequent fixation of adaptive structures, the so-called *inheritance of acquired characters*. The continued plasticity of amphibious plants and of beer yeast might be cited in favor of the former view, while the facts of progressive variability (p. 274),

[1] A less crude modern statement of this theory is that new conditions result in new functions, which in turn result in modified organs.

the retention of short vegetative cycles in plants from northern grown seeds, and the rigidity of many apparently adaptive characters, as in the xeromorphic structures of conifers, may be cited in favor of the latter view.

Apparently favoring the theory of adaptive response are the facts previously cited in connection with the development of cutin, cork, and air spaces, all of which are best developed where most useful. Cutin and cork are wanting in submersed aquatics, and they develop increasingly as the atmosphere becomes more desiccated, where their protective advantages become greater. Air spaces are best developed in submersed aquatics, where the difficulties in oxygenation are, perhaps, greatest, while they are least developed in xerophytes, where large air spaces would tend to facilitate excessive transpiration.

Associated with the adaptation theory is the doctrine of *use and disuse*, it being held that an organ develops most when most used, and least when least used. The best illustration that may be given of this is in the conductive tissues, where an abundant flow of material occasions maximum development, and where a slight flow, as in hydrophytes, occasions minimum development. There is no necessary association, however, between the adaptation theory and the theory of use and disuse; the conductive tracts that develop under the stimulus of parasitism might illustrate development through use, but they are very far from being adaptations.

The theory that plants are able to adapt themselves to new conditions is no longer tenable, being invalid *a priori* and disproven empirically. The hypothesis of adaptive response rests upon the same foundation as does the doctrine of *vitalism*, which postulates that there is something inherently different between lifeless and living matter. Each year the list of " vitalistic activities " of plants becomes more and more restricted through the establishment of a definite physical or chemical cause for what had been thought to have a vitalistic explanation, while never in the history of science has any phenomenon once explained on a physical or chemical basis been found later to be vitalistic. The same is true of adaptations; for example, tubers at one time were thought to be a provision made by plants for their vegetative offspring, but now it is known that they arise as a definite reaction to specific external conditions (p. 259). Similarly, many organs and structures now are known to result from definite conditions, and com-

parable explanations may be expected in the case of various organs whose cause is still unknown.

Many phenomena are out of harmony with the theory of adaptive response. Perhaps the best illustration of this is afforded by the reactions of plants that are attacked by parasites, where the conductive tissues are stimulated to increased development; obviously this is a most disadvantageous reaction, and the same may be said for the increased development of such tissues in xerophytes. In other cases galls are formed which accumulate quantities of food that may be very useful to the parasite, but certainly are harmful to the host. Nor does the adaptation theory account for the reactions of bast fibers, which develop best under xerophytic conditions, but are of little if any value in checking transpiration; they seem not to be stimulated by mechanical agents, though their chief value is mechanical. Conductive tissues and the velamen of orchid roots are most useful only when they are dead, and it is not easy to see how adaptation can arise through dying, nor how function here determines form, as adaptationists suppose.

Even instances commonly cited by teleologists as demonstrating adaptation often prove fallacious when analyzed. For example, root hairs, though lacking in a water medium where they are said not to be needed, are present in the same species in saturated soil, where their need is no more obvious; in dry soil or in concentrated media, where they are needed most of all, they fail to develop. Both in water and in dry soil, root hairs are absent, not because they are not needed, but because the conditions necessary for their development are absent. Similarly, palisade tissue, which has been thought to develop where the plastids need protection from intense sunlight, now is believed to have but little significance in this respect, since the palisade plastids of xerophytes have relatively slight motility. Nor are useless structures lost because they are useless, but only because the factors which induce them fail to operate. There are many obviously useless structures in plants, as the stamens of *Balanophora* (p. 433) and the cork wings of the sweet gum and of various elms; many other structures seem inconsequential, for example, many hairs (including stinging hairs) and spines. If the adaptation hypothesis is inadequate to explain the cases above noted, it is unnecessary elsewhere, since there are theories of causation which account equally well for the origin and survival of useless or moderately harmful structures and for the origin and survival of structures that are advantageous.

The theory of adaptive response is contrary to the current physical and chemical conceptions of the behavior of matter. Plants are made up of substances that react definitely to definite conditions, whether or not such reactions happen to be useful or harmful. If a new structure arises, it must be through some chemical or physical influence within the plant or in its environment. The adaptation theory, in implying that a plant responds only in an advantageous direction and in advantageous amount, endows the plant with a power of choice, and almost imagines it to survey the situation and to determine upon a course of action. It implies the possession of an inherent power to contravene the ordinary laws of nature. It presupposes a vital mechanism that holds adaptations in readiness for conditions that have not as yet occurred. And yet man himself possesses no such power of adaptation; he cannot "by taking thought add one cubit to his stature," though he can (as a plant cannot) study the laws of nature and place himself in such conditions as to facilitate desired reactions.

The theory of fortuitous variation. — The preceding considerations appear to show that protoplasm is not inherently adaptive. Disadvantageous structures (such as the food layers of galls or the enlarged conductive tracts of parasitized plants) or indifferent structures (such as cork wings and many hairs and spines) are quite as normal expressions of protoplasmic behavior as are the more numerous advantageous structures. The theory of *fortuitous variation*, which is based upon the laws of chance, postulates that newly developing structures are of all kinds: some advantageous, some disadvantageous, and some indifferent. The supporters of this theory are aligned in two general schools; the one school holds that new structures arise chiefly through the influence of external factors, while the other holds that factors residing within the plant itself are more important. Many investigators maintain that external factors are more important in some instances and internal factors in others; this composite view, embracing opinions of the two opposing schools, seems best able to explain the facts as they are now understood.

In the first place, variations are of frequent occurrence, though their supposed rarity once was given as an argument against the theory of evolution. Scarcely any species or any structure that has been studied carefully has been found to be invariable, and in some cases the amount of divergence from a supposed type is enormous. Not only do the individuals of a species as found in nature often differ from each other in

many particulars, but the same is true of individuals whose ancestry is known to be identical. An excellent illustration of such variation is seen in water cultures of various seedlings; while in such cultures maize roots commonly are hairless and wheat roots hairclad, certain maize roots may be hairclad or wheat roots hairless, though the conditions appear to be the same.

Congenital and reaction structures. — Structures (such as cork or cutin) which arise through reaction to environmental changes may be called *reaction structures*.[1] If a plant, when placed in xerophytic conditions, happens to develop as a reaction thereto such xerophytic features as cutinization, succulence, or dwarfness, it may be called a *reaction xerophyte;* similarly, there may develop *reaction mesophytes* or *reaction hydrophytes*. It is obvious, however, that many reaction structures cannot be classed as hydrophytic, mesophytic, or xerophytic; especially is this true of those that do not happen to be advantageous. Contrasting with reaction structures are those structures that are born with the species in whatever habitat it is developed (as in the case of mutations), and which are not lost if the species is grown in other habitats. Such structures may be termed *congenital structures*. If a species happens to be born with such xeromorphic features as succulence or dwarfness, it may be called a *congenital xerophyte;* similarly, there may develop *congenital hydrophytes* or *congenital mesophytes*, or plants that cannot be thus classed.[2] Thus any given structure, as a cutinized epidermal wall or a succulent cortex, may be a reaction structure in one species and a congenital structure in another species. Furthermore, any species may at the same time possess both variable reaction structures and fixed congenital structures, otherwise called adaptation and organization characters, careful experiment alone determining which is which. According to this theory, each plant association is composed of certain species that are fit because their critical features are the product of the habitat, and of other species that happen to have been born fit and thus enabled to survive.

Even congenital structures and organs are influenced by external factors. It has been seen that most stomata, hairs, and spines, if

[1] Too much emphasis cannot be placed upon the fundamental distinction between the word *reaction* and such words as *adaptation, adjustment, accommodation,* or *regulation*. The latter words imply an inherent power to change advantageously, while the word *reaction* implies no such power.

[2] Reaction and congenital xerophytes, mesophytes, and hydrophytes also may be termed, respectively, *facultative* and *obligate* xerophytes, mesophytes, and hydrophytes.

present at all, have a definite and fixed structure, and thus may be regarded as congenital rather than reactive. However, their presence or absence is determined by external agents, whence the latter are called *determinative factors*. Sometimes reference is made instead to *releasing factors*, the structure in question being regarded as potentially present, though its manifestation is inhibited until the proper factor enters in place of or in addition to the inhibiting factor. In the case of reaction structures it is believed that the form assumed, as well as the time and the place of appearance, is due to external agents, wherefore the latter are called *formative factors*.

While there is no doubt of the reality of reaction structures, because they are so readily capable of experimental production, there are many investigators who disbelieve in the reality of congenital structures. An alternative hypothesis is that all plant structures are or have been plastic. The so-called rigid or congenital structures may in some ancestral form have been as plastic as are the reaction structures of today; in this event the fixation of reaction structures has resulted in structures that now are congenital. It is equally possible that the supposedly rigid congenital structures really are plastic, but to an imperceptible degree, as compared with the leaf plasticity of amphibious plants; if this is true, all plant structures are plastic, some obviously and rapidly, and others so slightly or slowly that only experiments of long duration can reveal plasticity. While in the present state of imperfect knowledge, it is convenient and not necessarily incorrect to contrast reaction structures and congenital structures, it is possibly more correct to subdivide plant structures into those that certainly are plastic and those that apparently are rigid.

The survival of advantageous structures through natural selection.—While the origin of structures through reaction or through mutation cannot account for the present preponderance of advantageous structures and advantageous behavior, the theory of *natural selection* is in this respect as satisfactory as it has proven unsatisfactory from the standpoint of causation.[1] Of the species with new congenital structures, only those are likely to survive that happen to be suited for exist-

[1] Against natural selection as a causative theory may be urged: (1) the existence in many species of a capacity for advantageous regeneration, though the opportunity for such regeneration rarely if ever occurs in nature; (2) the existence of complicated structures (such as stinging hairs, digestive glands, and extra-floral nectaries) whose value to the plants possessing them is slight; and (3) the existence of "overadaptation," as in the flowers of orchids and in the seeds of certain xerophytes.

ence in the habitat in which the new structures develop, or that are able to migrate to a suitable habitat; a mesophyte that happens to originate in a desert or a plant suited to warm climates that happens to originate in a cold region cannot survive. Of the more plastic species only those are likely to survive which are able to react advantageously. Thus in the course of time it is to be expected that the plants that are congenitally unfit and the plants that react disadvantageously will largely be eliminated. Only occasionally would there survive plants with structures that are slightly disadvantageous. Somewhat more abundant might be the number of plants with indifferent or with only slightly useful structures. Many more individuals are born than have a chance to live, since severe physical conditions and crowding by other plants cause the elimination of the unfit and the survival of the fit; consequently advantageous structures must ultimately dominate, whatever the nature of the primitive structures. Such an explanation of the predominance of advantageous structures seems far more tenable than does the theory of origin through adaptation.

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Following each topic is the page of this volume to which reference is made, as (7). The authors to whom no reference is made other than by name are those mentioned in the General List, as HABERLANDT and GOEBEL I. The arrangement of authors under each topic is alphabetical, and the abbreviations of the various journals will be intelligible to any librarian or to any one acquainted with botanical and biological journals.

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